PHYLOGENETIC RELATIONSHIPS OF CERTAIN NEOTROPICAL TOADS WITH THE DESCRIPTION OF A NEW GENUS (ANURA: BUFONIDAE)

By Linda Trueb[1]

Abstract: A new bufonid genus, *Rhamphophryne*, is described. This genus contains five species (*Atelopus festae* Peracca, *Bufo rostratus* Noble, *Bufo nicefori* Cochran and Goin, and two new species, *R. acrolopha* and *R. macrorhina*), and ranges from extreme eastern Panamá to southern Ecuador. The genus is characterized by a reduced number of presacral vertebrae, a protuberant snout, highly modified hands and feet, and few, large, unpigmented eggs. In addition to these characters, the condition of the pectoral girdle and the cranial osteology seem to relate *Rhamphophryne* most closely to *Oreophrynella* and *Atelopus* in the new World. Morphological and zoogeographic evidence suggests that *Rhamphophryne* may have been derived from an ancestral *Bufo valliceps*-like stock. *Rhamphophryne* shares many specialized characters with Old World bufonids such as *Nectophryne, Pelophryne, Mertensophryne,* and *Laurentophryne*. It is suggested that these resemblances are the result of convergence rather than close phylogenetic relationship.

Among anurans, the bufonids have undergone an almost unparalleled, nearly cosmopolitan radiation; they are represented on all continents except Australia and Antarctica. As Tihen (1962) has pointed out, the family itself is difficult to define, and parallel differentiation within the family has consistently frustrated attempts to establish meaningful taxonomic subdivisions limited to either the New World or Old World. Within the New World, Tihen (1962) has proposed a systematic arrangement of five species groups of *Bufo* based principally on osteological criteria. This study is a valuable contribution to an understanding of the more generalized, widespread New World representatives of *Bufo*. There is, however, a significant number of more specialized bufonids (including Atelopodidae *auctorum*) of less widespread geographical distributions. Of particular interest are those restricted to montane environments. Some of these taxa are presently included in the genus *Bufo (rostratus, periglenes, fastidiosus, holdridgei, simus, coerulescens);* their inclusion within this genus probably represents a taxonomic convenience rather than a significant phylogenetic placement. In contrast, other montane taxa, more recently investigated or having more obvious morphological specializations (e.g. *Oreophrynella, Crepidophryne*), have been relegated to separate genera. The relationships of these taxa to one another and to other bufonids of the New World and Old

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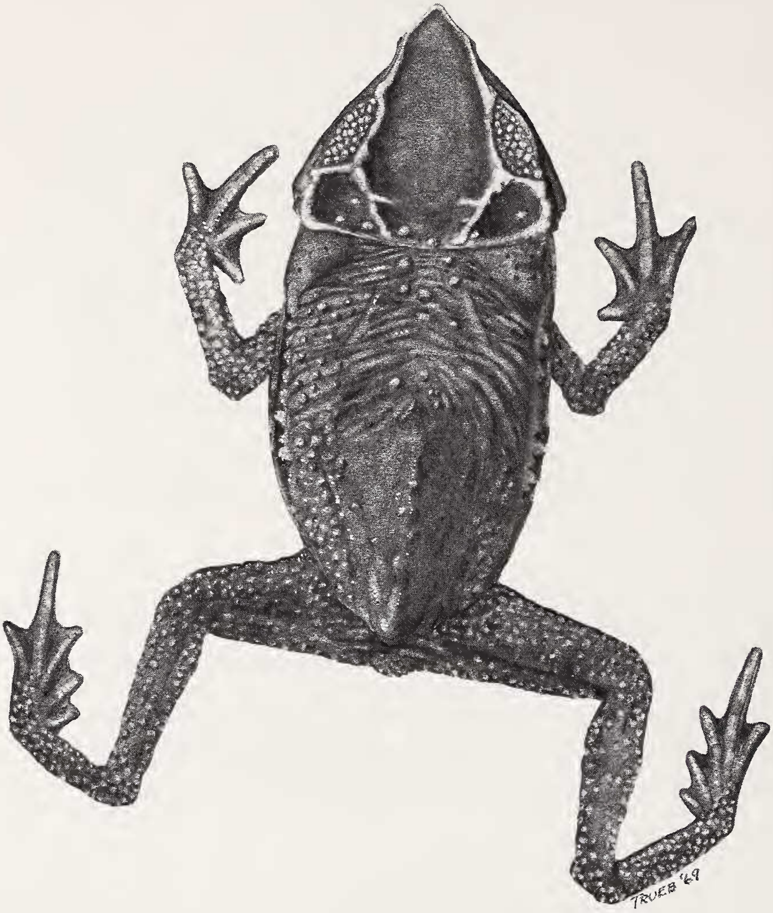

FIGURE 1. Dorsal view of paratype of *Bufo rostratus* (=*Rhamphophryne macrorhina*), ♂ (AMNH 1384). × 2.

World have been largely ignored. The present paper presents the descriptions of a new genus and two new species, and offers comments on the relationships and zoogeography of some of the Neotropical, montane bufonids.

Noble (1920) described a new species of small toad (*Bufo rostratus*) on the basis of three specimens from the southern part of the Departamento de Antioquia, Colombia. The type series consists of the holotype, an adult male, and two paratypes, an adult male and a juvenile of undetermined sex. Noble distinguished *B. rostratus* from other species of *Bufo* on the bases of the following characters: (1) snout produced into a three-edged rostrum; (2) paro-

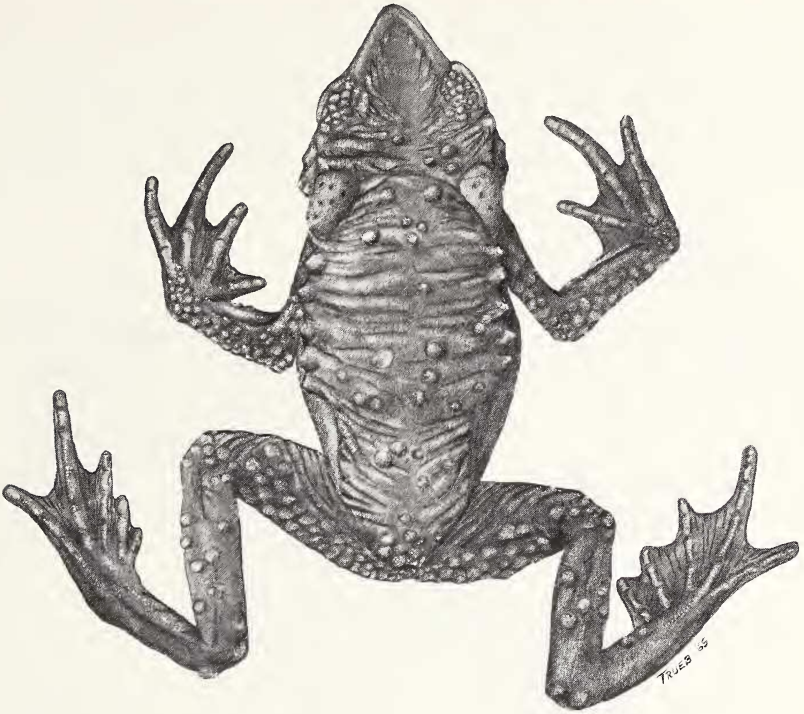

FIGURE 2. Dorsal view of holotype of *Bufo rostratus* (=*Rhamphophryne rostrata*), ♂ (AMNH 1359). × 1.5.

toid glands triangular, not longer than greatest diameter of the eye; (3) tympanum hidden; (4) fingers one-third, and toes one-fourth webbed; (5) tarsal fold absent; (6) prominent series of large tubercles along each side of back. More recently, Cochran and Goin (1970) redescribed *Bufo rostratus* and named a new subspecies. *Bufo rostratus nicefori*, based on five specimens, also from the Departamento de Antioquia, Colombia.

My re-examination of Noble's type series revealed that the adult male paratype (Fig. 1) of *Bufo rostratus* is clearly a different species than the holotype (Fig. 2) and juvenile paratype. Comparison of these specimens with the redescription of *Bufo rostratus rostratus* provided by Cochran and Goin (1970) indicates that they based their redescription on the adult paratype, rather than on the holotype of *Bufo rostratus*.

There is no doubt that both species represented in the type series of *Bufo rostratus* are closely related and that Cochran and Goin's *Bufo rostratus nicefori* is closely allied to them. A series of small toads, recently acquired from eastern Panamá, and *Atelopus festae*, known from southern Ecuador, represent two other specifically distinct forms which show striking similarities to the *Bufo rostratus* group from Colombia.

Many characteristics shared by these five taxa are unique among the currently recognized bufonids. Adults are all relatively small, ranging from 32 to 51 mm in snout-vent lengths. There are seven or eight presacral vertebrae included in the vertebral column, and the sacrum is either fused to the coccyx

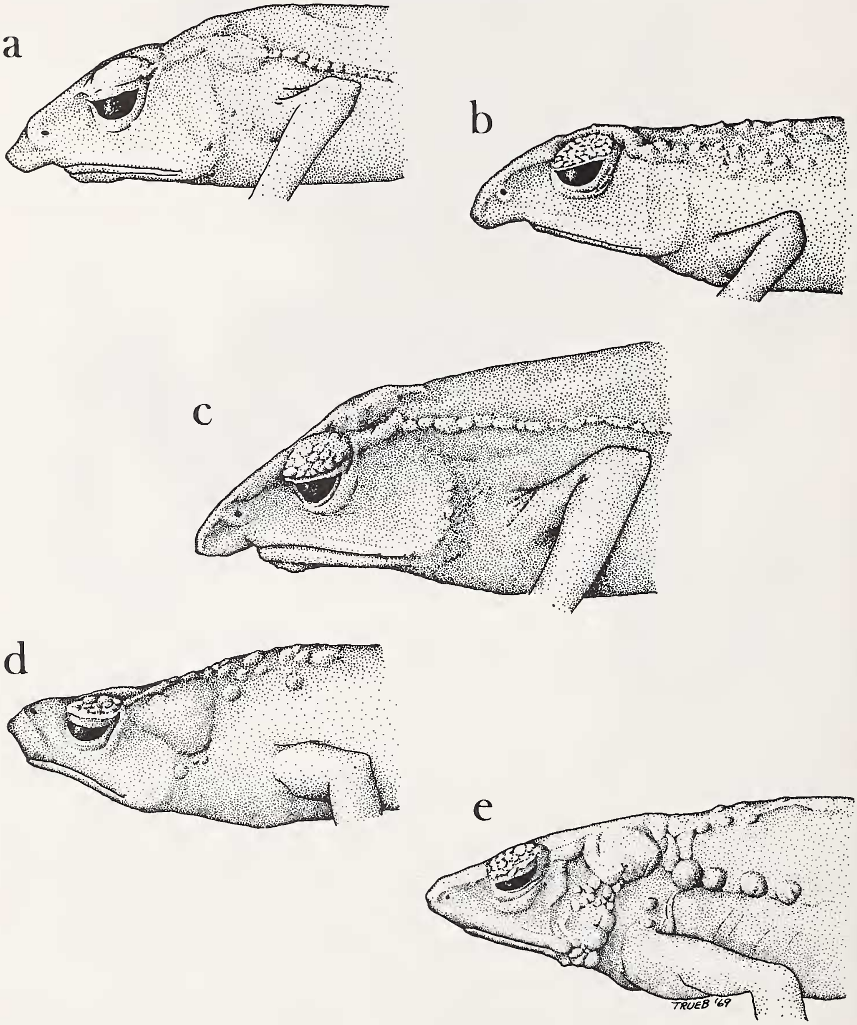

FIGURE 3. Lateral views of heads of *Rhamphophryne:* (a) *R. acrolopha,* ♂ (KU 76965); (b) *R. festae,* ♂ (CAS 11417); (c) *R. macrorhina,* ♀ (LACM 44394); (d) *R. nicefori,* ♀ (USNM 163476); (e) *R. rostrata,* ♂ (AMNH 1359). × 1.6.

or articulated with it by a very weak bicondylar or a monocondylar articulation. The adductor longus muscle is absent, as are the annulus tympanicus and columella. All species except one (for which data are not available) have large, unpigmented eggs, which are few in number. Members of this group have heavily ossified, triangular heads which are produced into distinctive, anteriorly protruding snouts. The foregoing combination of characters indicates a close

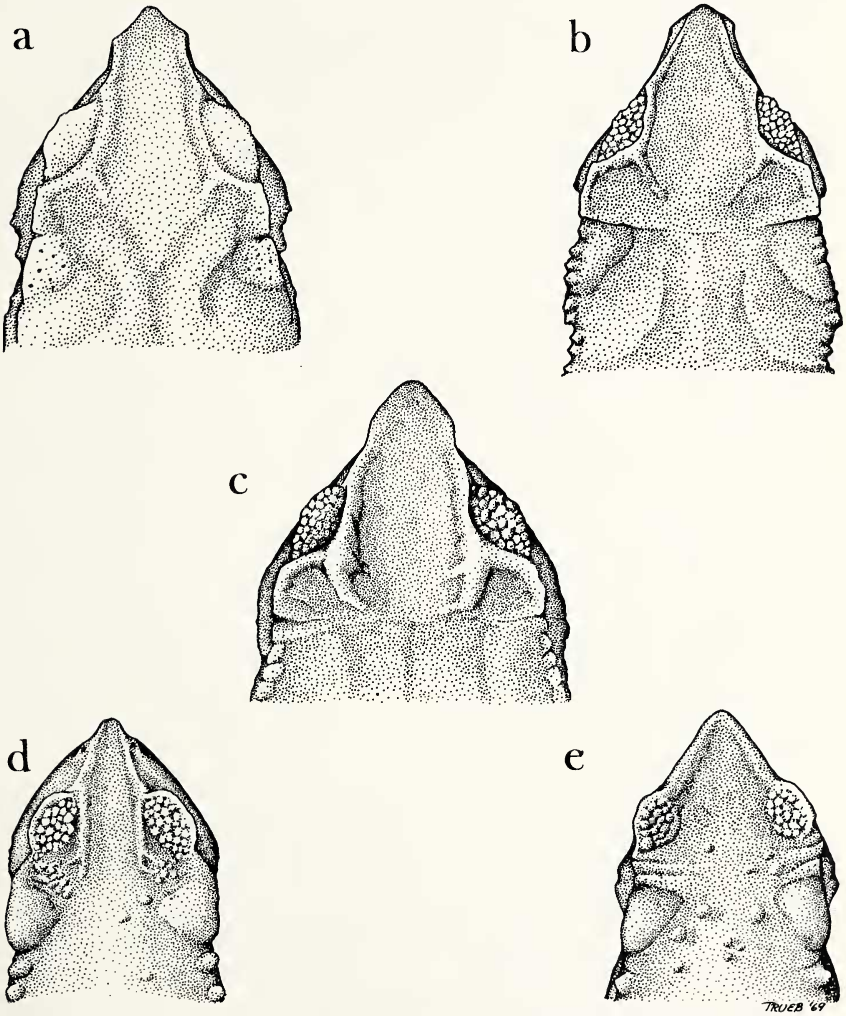

FIGURE 4. Dorsal views of heads of *Rhamphophryne:* (a) *R. acrolopha,* ♂ (KU 76965); (b) *R. festae,* ♂ (CAS 11417); (c) *R. macrorhina,* ♀ (LACM 44394); (d) *R. nicefori,* ♀ (USNM 163476); (e) *R. rostrata,* ♂ (AMNH 1359. × 1.6.

relationship among the four taxa mentioned and clearly distinguishes them as a group from the genus *Bufo,* which is characterized by eight presacral vertebrae, a bicondylar sacral-coccygeal articulation and many, small, pigmented eggs. On the bases of these distinctions and with reference to the peculiar cranial condition shared by these five taxa, they are here referred to a new genus.

Rhamphophryne, new genus

Type species.—Rhamphophryne acrolopha, new species.

Diagnosis.—These small bufonids can be distinguished from other members of the family by the following combination of characters: (1) seven or eight independent presacral vertebrae; (2) sacrum fused to coccyx or sacrum having a monocondylar or very weakly bicondylar articulation with coccyx; (3) cervical and second presacral vertebrae not fused; (4) omosternum absent; (5) protruding snout produced by extended ossification of anterior part of sphenethmoid and nasal cartilages; (6) presence of partial integumentary-cranial co-ossification; (7) tips of phalanges not expanded; (8) parotoid gland present; (9) adductor longus muscle absent; (10) eggs large, unpigmented, few in number; (11) annulus tympanicus and columella absent; and (12) arciferal pectoral girdle.

Content.—Five species, as follows: *Rhamphophryne acrolopha, new* species, *R. macrorhina,* new species, *Bufo rostratus* Noble, *Bufo rostratus nicefori* Cochran and Goin, and *Atelopus festae* Peracca.

Description.—General morphology. The snout in profile (Fig. 3) protrudes beyond the upper jaw and in dorsal aspect is acuminate (Fig. 4). Loreal region is concave, and nostril is lateral, protuberant and located ventral to the canthal ridge. Pupil is horizontally elliptical. The tongue is longer than wide and free posteriorly. Choana is small, ovoid and lateral in position. Prevomerine teeth are absent. Vocal slits are variable in occurrence. All members of this genus have well defined canthal ridges and supraorbital crests. Postorbital, supratympanic, pretympanic and occipital crests vary in appearance and degree of development.

The forelimbs and hind limbs vary from slender to robust; all lack folds. Axillary membranes are absent. Although the hands and feet have the common phalangeal formulae of 2-2-3-3 and 2-2-3-4-3, respectively, they are highly variable with regard to other characters (Figs. 5 and 6). The digits are short and robust in *nicefori* and elongate and slender in *rostrata* and *acrolopha.* Fingers and toes are nearly fully webbed in some species and vestigially webbed in others. Supernumerary tubercles are present in all species, but variable in their abundance. Subarticular tubercles, large and well developed in three species, are replaced by lamellar, padlike swellings in *macrorhina* and *nicefori.* Palmar and metatarsal tubercles are characteristic of all species but variable in their occurrence and appearance in *nicefori.*

The cloacal openings are directed posteriorly or posteroventrally at the mid- or upper levels of the thighs. Only one species, *nicefori,* has an cloacal sheath. Parotoid glands vary in appearance from scarcely discernible in *festae* to large and smooth in *nicefori.* Tubercles are small and conical in *macrorhina, acrolopha,* and *festae,* but large and rounded in *rostrata* and *nicefori.* All species have characteristic dorsolateral rows of tubercles extending from the posterior margin of the head or parotoid gland posteriorly along the flanks, and small, round tubercles covering the eyelids. They tend to have a proliferation of tubercles on the dorsal surfaces of the limbs.

Osteology.—The skulls (Figs. 7 and 8) of *Rhamphophryne* are triangular in dorsal and ventral views and broader than long. Only one specimen of each of three species, viz. *Rhamphophryne acrolopha, macrorhina,* and *festae* is available for detailed ostelogical study; other osteological data were obtained by dissection and/or examination of stereo radiographs. The cranial measurements and ratios (Table 1) show that the shapes of the skulls of these species conform closely to one another. Both *acrolopha* and *festae* have skulls which are obviously wider than long, whereas in *macrorhina,* a species nearly equivalent in size to *acrolopha,* the skull length nearly equals the width. Similarly, the skulls of *festae* and *macrorhina* are somewhat narrower with respect to their heights than is that of *acrolopha.* These figures tentatively suggest that *acrolopha* has, proportionally, the broadest skull of the three species.

TABLE 1. Skull measurements in *Rhamphophryne*

Species	HL (Head Length) mm	HW (Head Width) mm	H (Height) mm	H/HL	H/HW	HL/HW
acrolopha	16.8	18.6	9.0	0.536	0.484	0.903
macrorhina	13.8	14.1	8.0	0.570	0.567	0.979
festae	10.3	11.4	6.3	0.612	0.553	0.904

Complete integumentary-cranial co-ossification does not occur in this genus. The skin is movable on those smooth areas of the skull which are not exostosed. Skin overlying rugose, exostosed areas such as the cranial crests, canthal ridges, and anterior margins of the orbits is partially adherent. It is likely that a similar, partially co-ossified situation prevails in *Rhamphophryne* as was described for the partly co-ossified hylid frog, *Osteocephalus taurinus* (Trueb, 1970). If this assumption is correct, the exostosed portions of the skulls of *Rhamphophryne* have probably been laid down in the lower, dense connective tissue layer of the overlying skin, thereby causing partial adherence of the overlying dermis to the skull beneath.

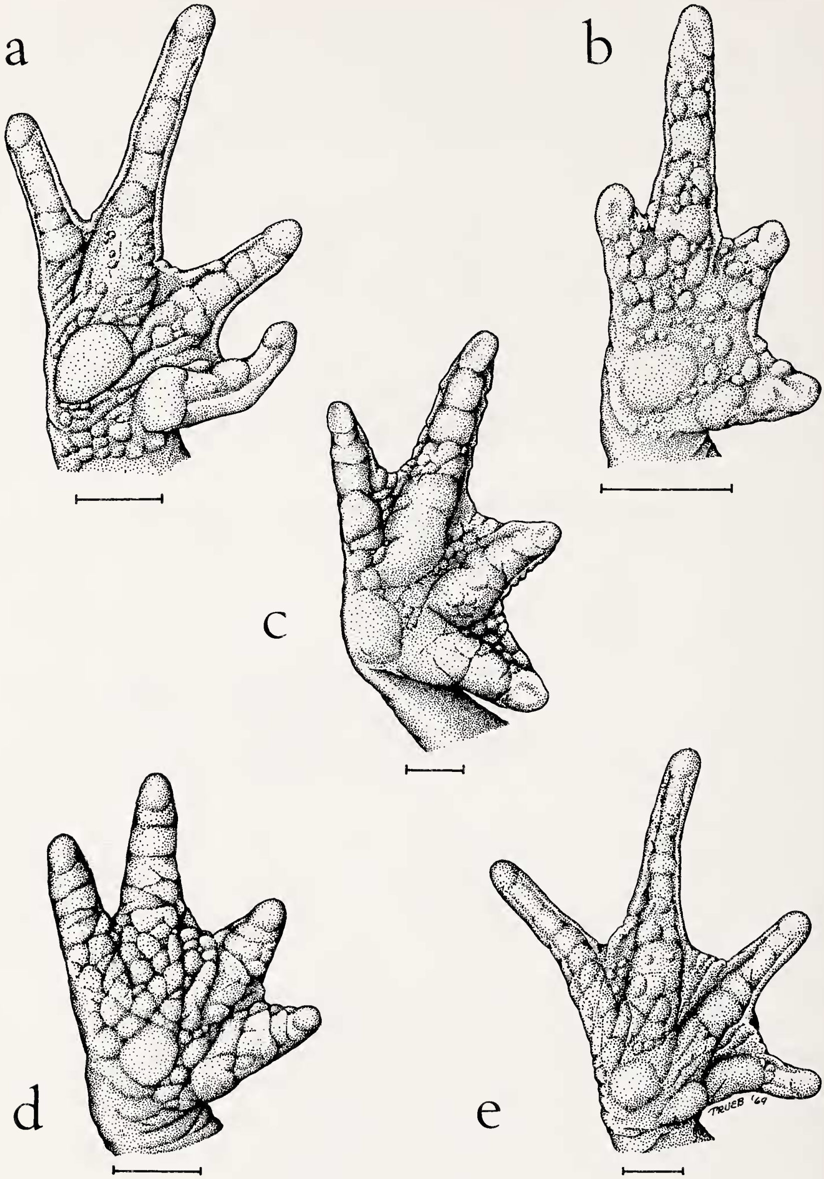

FIGURE 5. Palmar views of right hands of *Rhamphophryne:* (a) *R. acrolopha,* ♂ (KU 76965); (b) *R. festae,* ♂ (USNM 167175); (c) *R. macrorhina,* ♀ (LACM 44394); (d) *R. nicefori,* ♀ (USNM 163476); (e) *R. rostrata,* ♂ (AMNH 1359). Lines equal 2 mm.

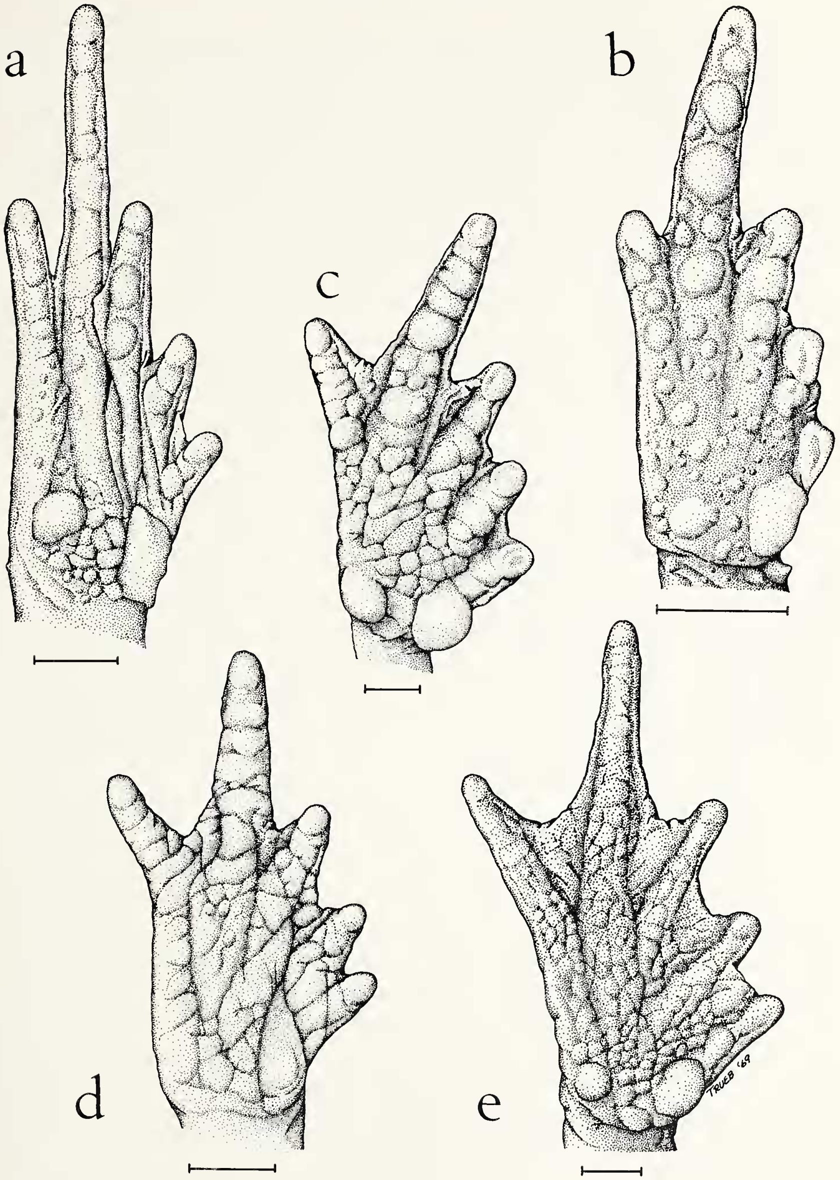

FIGURE 6. Plantar views of right feet of *Rhamphophryne:* (a) *R. acrolopha,* ♂ (KU 76965); (b) *R. festae,* ♂ (USNM 167175); (c) *R. macrorhina,* ♀ (LACM 44394); (d) *R. nicefori,* ♀ (USNM 163476); (e) *R. rostrata,* ♂ (AMNH 1359). Lines equal 2 mm.

The premaxillaries are separated medially by connective tissue. A conspicuously long, pointed palatine process is present posteromedially on each premaxillary (Fig. 7b). The alary processes of the premaxillaries are widely separated medially by the anterior end of the sphenethmoid; they are inclined anteriorly (Fig. 8), and laterally deflected in at least two species (*acrolopha* and *macrorhina*). The length of the alary processes varies from two times (*acrolopha and macrorhina*) as long as the depth of the pars dentalis of the premaxillary to two and one-half times (*festae*).

In ventral view (Fig. 7b), the prevomers lie well lateral to the midlines of the skulls. The anterior ends lie adjacent to the anterior ends of the partes palatinae of the maxillaries. The posterior ends of the prevomers lie ventrally adjacent to the sphenethmoid in *festae* and *acrolopha;* in *macrorhina* the entire prevomer lies laterally adjacent to the anterolateral margin of the sphenethmoid. The anterolateral wings of the prevomers form the anteromedial margins of the choanae; this wing is reduced in size in *macrorhina.* The posteromedial margins of the choanae are formed partially by the sphenethmoid; the posterolateral prevomerine wings are medially deflected in *macrorhina* and *acrolopha* and reduced to tiny spurs in *festae.* The prevomers of these three species are edentate; prevomerine teeth are also absent in *rostrata* and *nicefori.* Palatine bones are present in all species of *Rhamphophryne;* the bones are narrow and lie posterior to the internal nares. In *macrorhina, acrolopha,* and *festae* the distal ends of the palatines are only slightly expanded and articulate with the posterior processes of the partes facialae of the maxillaries and the maxillary processes of the nasals. Proximally the palatines articulate with the sphenethmoid. The palatine is smooth in *macrorhina,* bears a weak longitudinal ridge in *festae* and a slightly irregular ridge in *acrolopha.*

The nasals (Figs. 7a and 8) are large, extending anteriorly beyond the level of the mandibular arch to terminate at about the level of the anterodorsal tips of the alary processes. In *macrorhina* and *acrolopha,* the nasals converge medially throughout most of their lengths and are entirely underlain by the ossified sphenethmoid. In *festae* the nasals are medially separated throughout their lengths and extend considerably beyond the anterior terminus of the bony sphenethmoid. The nasals arch posterodorsally over the external nares and terminate posteroventrally in slender maxillary processes which articulate with the palatines and posterior processes of the partes faciales of the maxillaries. The posterior nasal margins bordering the orbits are slightly exostosed in *acrolopha* and *festae,* but smooth in *macrorhina.* Dorsally, the posterior edges of the nasals of all three species articulate with the anterior margins of the frontoparietals.

The maxillary is moderately robust in *acrolopha* and less well developed in *macrorhina* and *festae.* The partes faciales are moderate in size and do not articulate with the nasals, except posteriorly in *macrorhina* and *acrolopha;* in *festae,* the pars facialis is reduced with only the posterior process remaining.

Ventromedially, the partes palatinae of the maxillaries of all three species are inconspicuous. The maxillaries articulate firmly with the short, stout quadratojugals posteriorly at approximately the level of the prootic foramen.

The frontoperietals (Fig. 7a) converge medially throughout their lengths. Anteriorly, they articulate with the posterior margins of the nasals and join with the posterodorsal corners of the nasals to form upturned supraorbital crests. Posteriorly, the frontoparietals extend laterally over the epiotic eminence areas of the cristae paroticae to form the medial portions of the postorbital crests. The occipital ridge is scarcely discernible in *festae;* it is represented by a low thickening which borders the medial edge of the open carotid canal and is formed in the dorsal surface of the frontoparietal. The occipital ridge is somewhat better developed in *acrolopha;* irregularly exostosed spurs of bone arch over the carotid canal and partially roof it. In *macrorhina* the occipital crest is prominent; it forms a complete roof over the carotid canal. The frontoparietals articulate with the squamosals dorsal to the cristae paroticae and seem to be fused with the prootics in each species, although this character is difficult to assess without examination of sectioned material.

The most striking cranial feature of *Rhamphophryne* is the development of the sphenethmoid and its associated cartilages. Again, the nature of this unusual characteristic is difficult to describe adequately without having studied serial cross-sections. In lieu of such an opportunity, one is forced to extrapolate on the bases of previous studies. In the majority of anuran skulls, the endochondral sphenethmoid is in synosteotic continuity with the septum nasi anteriorly. Associated with the septum, which forms the medial wall of the nasal cavities, are various other cartilages such as the tectum nasi (roof of the nasal cavities) and solum nasi (floor of the nasal cavities). The cartilage forming these elements is continuous with that in which the sphenethmoid is laid down. Usually the anterior parts associated with the nasal cavities remain cartilaginous, whereas the posterior part ossifies to varying degrees, forming a casing for the anterior part of the brain; this is commonly known as the sphenethmoid. In *Rhamphophryne acrolopha* and *macrorhina* (and, presumably, also in *nicefori* and *rostrata*) the ossification of the sphenethmoid is continuous anteriorly with completely or nearly completely ossified nasal septa and their associated cartilages. There seems to have been a proliferation of the cartilaginous anterior end of the nasal septum, producing the protuberant snout characteristic of this genus. This area is subsequently ossified in *acrolopha* and *macrorhina* to produce the bony snout of the adult. A similar situation prevails in *festae,* except that the anterior end of the snout remains cartilaginous in all but the largest adults.

The anterior extension of the snout in this genus has resulted in some secondary modifications of cranial structure. As the snout grows forward during development, it evidently causes the anterior rotation of the alary processes of the premaxillaries so that the processes come to be anteriorly

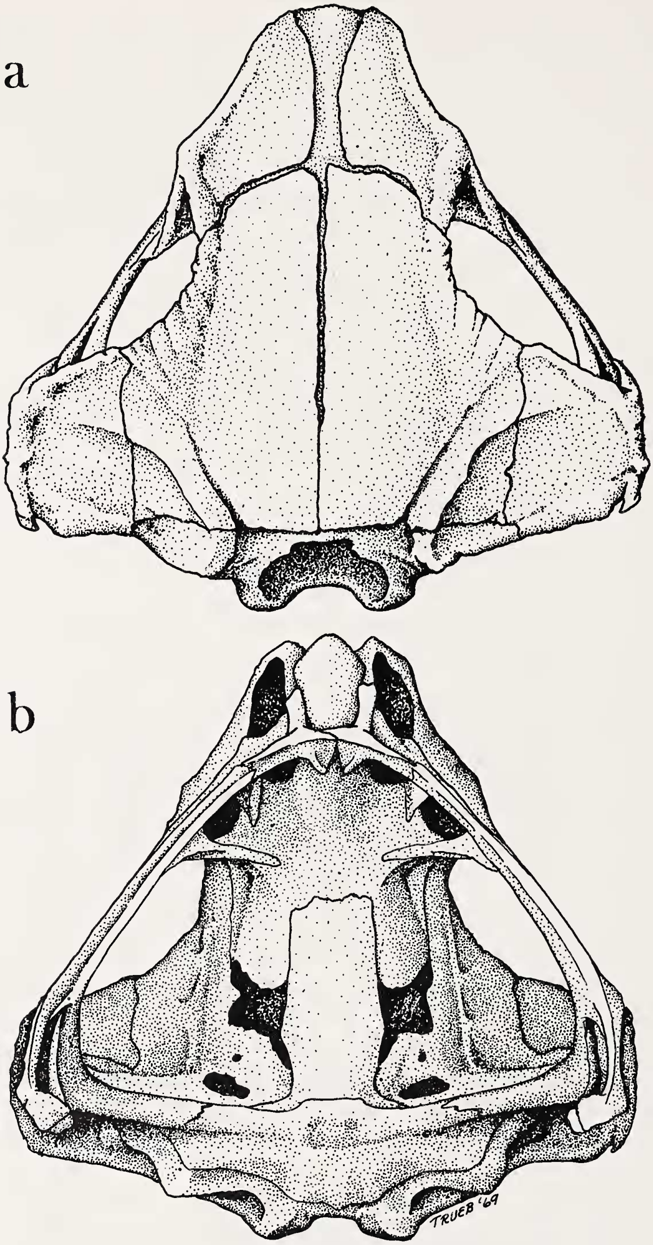

FIGURE 7. Skull of *Rhamphophryne festae*, ♀ (USNM 167168); (a) dorsal; (b) ventral. × 7.

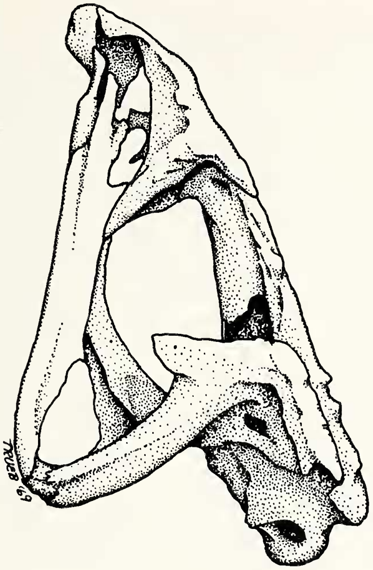

FIGURE 8. Skull of *Rhamphophryne festae,* ♀ (USNM 167168): in lateral view. × 7.

inclined (*macrorhina* and *acrolopha*) or nearly horizontally oriented (*festae*; Fig. 8). In *macrorhina* and *acrolopha,* the alary processes are laterally deflected, presumably as a result of the thickening of the anterior end of the septa nasi. Examination of preserved specimens of this genus shows that the nostrils are located anterior to the position one would normally anticipate with respect to the anterior limit of the upper jaw. Because the external nares usually lie posterior to the anterior levels of the nasal cavities, the position of the nostrils suggests that the nasal structures have expanded or moved forward to occupy a more anterior position in the extended snouts.

Modifications of this kind are not unknown among other anurans. Similar phenomena have been described by Lynch (1971) for the *fuscus* group of *Leptodactylus* and by Trueb (1970) in the casque-headed hylids. There is, however, one striking difference which should be noted in the hylids. The addition of new bones to produce protuberant snouts in the hylids and the proliferation of existing cranial structures have been derived by modifications of the highly plastic dermal elements. The kinds of changes which have occurred in *Rhamphophryne* have been produced by proliferation and increased ossification of endochondral elements.

The sphenethmoid (Fig. 7b) is not extensively ossified posteriorly, especially in *macrorhina.* In this species, the bony part of the sphenethmoid terminates a short distance posterior to the level of the palatines, thereby creating a particularly large, unossified area around the optic foramen. The sphenethmoid is better ossified posteriorly in *festae* and *acrolopha.*

The parasphenoids of all three species are very similar. The bones are edentate and truncate anteriorly. In *festae* and *acrolopha* the anterior end of the bone lies ventral to the sphenethmoid, just posterior to the level of the palatines, whereas in *macrorhina* the anterior terminus lies more posterior and articulates with the posterior bony margin of the sphenethmoid.

The squamosals (Fig. 8) are robust. The anterior arms are short, broad spurs which project one-fourth, or less, of the distance from the dorsal union of the three squamosal arms to the maxillary. An inconspicuous pretympanic crest in some specimens of *acrolopha* and *macrorhina* forms by thickening of this squamosal element. The posterior arms lie adjacent to, and do not extend beyond, the distal edges of the cristae paroticae. In dorsal view the posterior squamosal arm broadly overlaps the crista parotica and articulates at least partially with the frontoparietal. Along the anterior edge of the crista, the overlapping portion of the squamosal is exostosed to form a postorbital ridge; similarly, along the lateral margin of the crista, the squamosal forms a supratympanic crest. The ventral squamosal arms are particularly robust. Each arm bears a broad articulation with the posterior ramus of the pterygoid medially and the quadratojugal laterally.

There is little variation among the pterygoids. Each species has a well-developed pterygoid (Fig. 7b), in which the posterior ramus articulates with the squamosal, and the medial ramus broadly overlaps the parasphenoid posterolaterally. The anterior pterygoid rami of *festae* and *acrolopha* articulate laterally with the maxillaries and anteriorly with the distal end of the palatines. The anterior pterygoid ramus of *macrorhina* is shorter, articulating only with the maxillary laterally.

The prootic and exoccipital bones are well ossified and, as previously mentioned, apparently fused with the frontoparietal. Bony oculomator, prootic, and jugular foramen are evident. All vestiges of the columella are lost, and the lateral portions of the otic capsule are cartilaginous.

The occipital condyles are closely juxtaposed rather than widely separated. Similarly, the cervical condyles are closely juxtaposed as in all other bufonids (Lynch, 1969). There are seven or eight presacral vertebrae which bear moderately long transverse processes (Fig. 9). In an anterior to posterior sequence, the widths of the transverse processes from narrowest to widest are 2-7-6-5-3-4 in those species having seven presacral vertebrae. In *macrorhina* the widths of the transverse processes are 2-8-7-6-5-3-4. The transverse processes of the second presacral vertebrae are directed anteriorly. Those of vertebrae three through six in *nicefori, festae,* and *acrolopha,* three through seven in *macrorhina,* and three through five in *rostrata* are directed posteriorly. Transverse processes of vertebrae six and seven are directed anteriorly in *rostrata.* Those of the seventh vertebrae in *nicefori, festae,* and *acrolopha* and

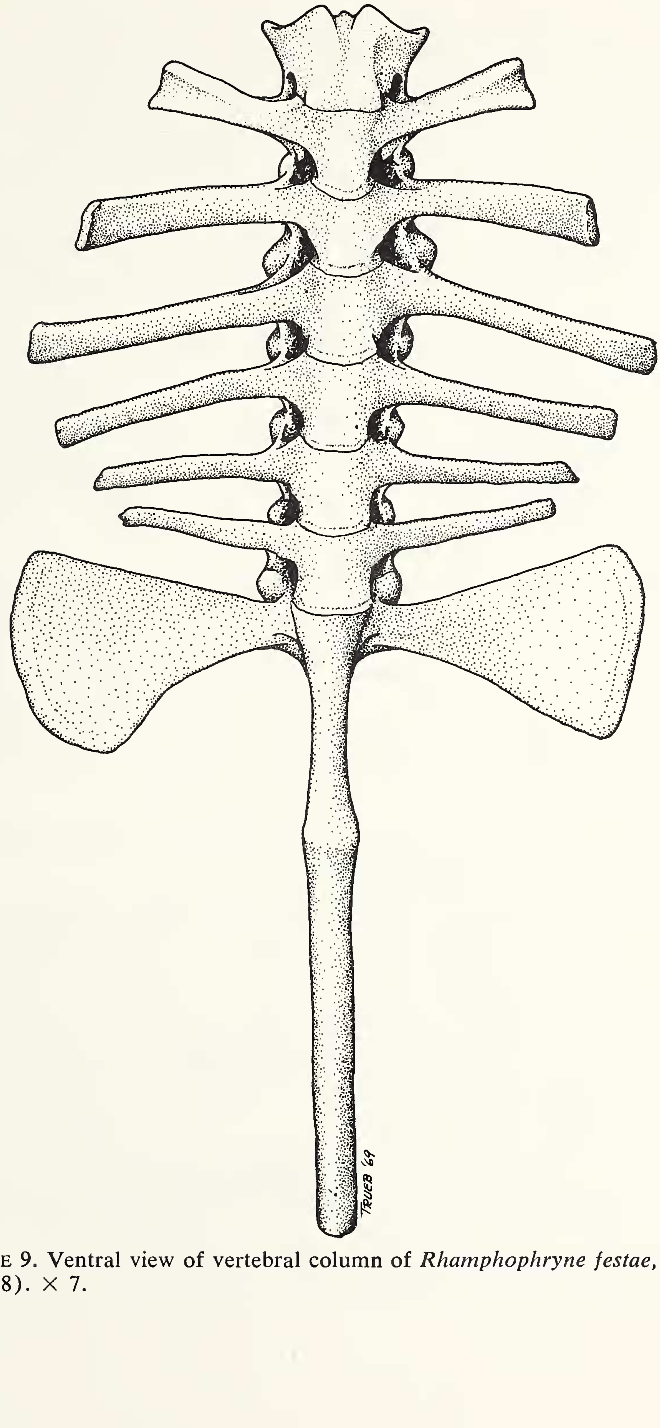

FIGURE 9. Ventral view of vertebral column of *Rhamphophryne festae*, ♀ (USNM 167168). × 7.

the eighth in *macrorhina* are directed anteriorly. The sacral diapophyses of all species are expanded. In *festae* and *rostrata* the sacrum and coccyx are fused. In *nicefori* and *acrolopha* the sacrum bears a monocondylar articulation with the coccyx, whereas in *macrorhina* the articulation is very weakly bicondylar. The coccyx bears no noticeable lateral expansion in any of the species.

The omosternum is absent in this genus, as it is in all other bufonids except *Nectophrynoides* and toads of the *Bufo haematiticus* group. The pectoral girdle is arciferal but tends to have a broad epicoracoid bridge. The sternum is cartilaginous. The ilia bear no notable prominences or crests. The limb elements are relatively slender. The phalanges are markedly reduced in length in *festae,* but of normal extent in other species.

Myology.—The adductor longus muscle is absent in the thighs of all species of *Rhamphophryne.* The length of the tensor fasciae latae muscle is somewhat variable. The muscle is short in *acrolopha, macrorhina,* and *rostrata;* it originates from a point about one-fourth the distance from the proximal end of the ilium and inserts on the surface of the cruralis-gluteus complex. In *festae* and *nicefori* the tensor is longer; it originates at approximately the midlength of the ilium.

Natural history.—Little is known concerning the habits and life history of this genus. All species (with the possible exception of *Rhamphophryne rostrata* for which there are no data available) have few, large, unpigmented eggs. No tadpoles have been associated with the genus. Although vocal slits are present in the males of three species (*nicefori, macrorhina,* and *rostrata*), none has been observed to call. The available field notes suggest that members of this genus are diurnal; all specimens have been obtained from the forest floor by day. Significantly, none (including gravid females) has been recorded as having been found near water.

Etymology.—The generic name is derived from the Greek words *rhampho,* meaning beak, and *phryne,* meaning toad, with reference to the protuberant snout characterizing this group of bufonids.

Distribution.—Members of this genus occur at moderate elevations in the mountains of northern Colombia and extreme eastern Panamá, and on the lower Andean slopes and in the upper Amazon Basin of Ecuador (Fig. 10).

Remarks.—On the basis of external characters, members of the genus *Rhamphophryne* are easily confused with juveniles of *Bufo typhonius.* Toads of the latter species are widespread, occurring throughout the Amazon Basin, in northwestern South America, and eastern Panamá. *Bufo typhonius* generally is found at moderate to low elevations (up to 800 m). All specimens of *Rhamphophryne* have been collected at elevations exceeding 800 m except *festae,* which apparently occurs sympatrically with *Bufo typhonius* in Amazonian Ecuador. Adult *Bufo typhonius* are easily distinguished from *Rhamphophryne* by their much greater size, less protuberant snouts, broad alate processes of the squamosal dorsally, and conspicuous tympani. However, in smaller individuals of this species, the snouts are proportionally

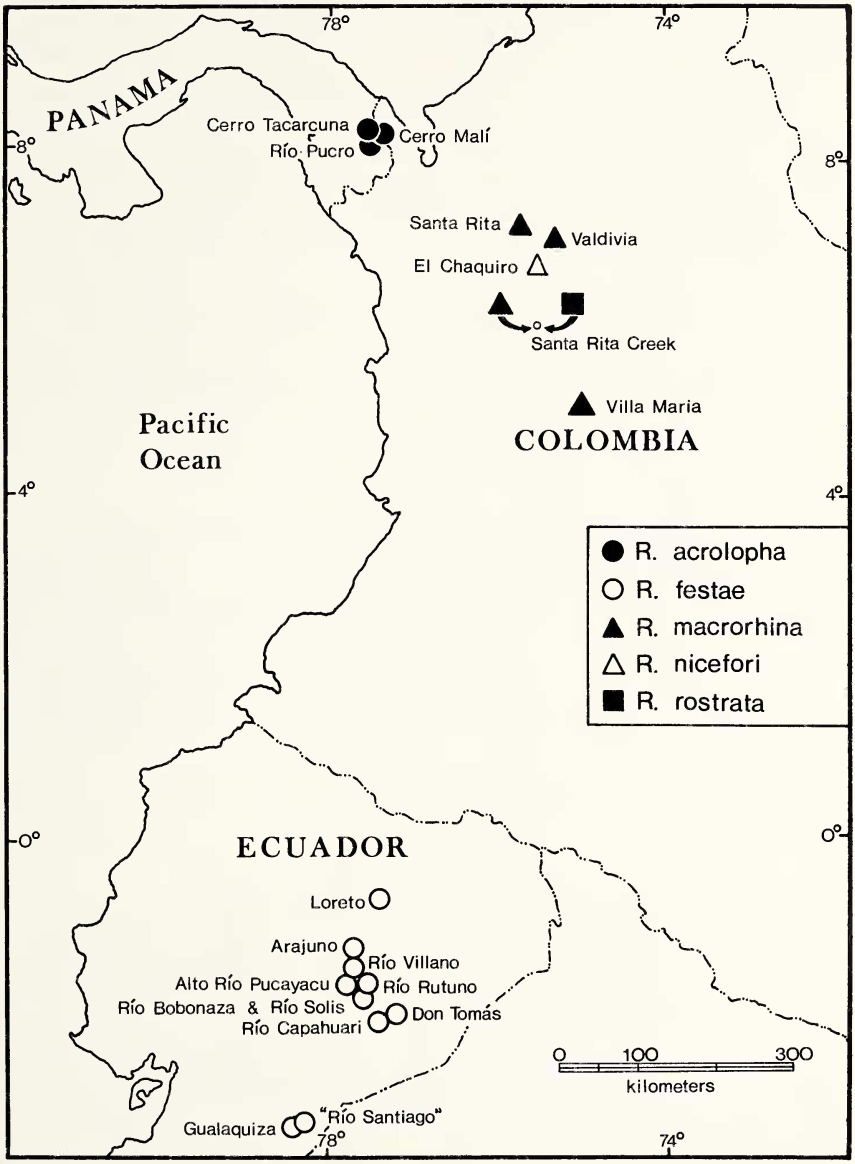

FIGURE 10. Map of Panamá, western Colombia and Ecuador, showing locality records of *Rhamphophryne*.

more protuberant, the squamosal processes poorly developed, and the tympani much less evident. Although inconspicuous in some individuals, the presence of a tympanum consistently distinguishes *Bufo typhonius* from all members of the genus *Rhamphophryne.*

Some comment should be made concerning the relationship of *Rhamphophryne* with a group of small, earless, montane bufonids found at elevations above 1000 meters in Costa Rica and western Panamá. Included in this group are *Bufo periglenes, fastidiosus, holdridgei,* and *Crepidophryne epioticus.* Two other species (*Bufo coerulescens* and *simus*) often have been mentioned in conjunction with these taxa. *Bufo coerulescens* is known only from two type specimens of doubtful maturity, and the type of *simus* is apparently lost. A great deal of confusion exists concerning the relationships among all of these species and of these with other bufonids. Hopefully, a thorough study will elucidate these problems; however, until such work appears, it should be pointed out that *Rhamphophryne* is morphologically distinct from these toads.

KEY TO THE SPECIES OF *RHAMPHOPHRYNE*

1. Hands with long, free fingers 2
   Hands palmate 3
2. Dorsolateral tubercles small, depressed, in continuous row; snout directed anteroventrally; cranial crests moderately developed . . . . *acrolopha*
   Dorsolateral tubercles large, conical, in discontinuous row; snout directed anteriorly; cranial crests weak or absent . . . . *rostrata*
3. Dorsolateral tubercles small, depressed in continuous row; occipital crests well developed . . . . *macrorhina*
   Dorsolateral tubercles moderate-sized, conical, not in continuous row; occipital crests weak 4
4. Third finger much longer than others . . . . *festae*
   Third finger only slightly longer than others . . . . *nicefori*

ACCOUNTS OF SPECIES

Rhamphophryne acrolopha, new species

Holotype.—Adult male, University of Kansas Museum of Natural History (KU) 76965 from Cerro Malí, Darién Province, Panamá, elevation 1410 m; obtained on July 12, 1963, by William E. Duellman.

Paratypes.—KU 76961-4 and UMMZ 129694-5 obtained with the type, MLS 1240 and LACM 54337-8 obtained on July 10 and 11, 1963, by William E. Duellman; USNM 151075-6 from elevations of 1265 and 1451 m on Cerro Malí, and USNM 151101, 151104-5, and 151107 from Cerro Tacarcuna, Darién Province, Panamá, between elevations of 1265 and 1481 m, obtained between January 29 and March 1, 1964, by Charles O. Handley, Jr.

Diagnosis.—A moderate-sized *Rhamphophryne* (♂ 38 mm, ♀ 45 mm) which can be distinguished from other members of the genus by the following combination of characters: (1) seven presacral vertebrae; (2) sacral vertebra not fused with coccyx; (3) snout long, protuberant, and directed anteroventrally; (4) cranial ornamentation moderately developed; (5) supraorbital, postorbital and supratympanic crests present; (6) pretympanic crest variable in occurrence; (7) occipital crest present but indistinct; (8) dorsal tubercles small and conical; (9) dorsolateral tubercle row small, depressed, extending from posterior margin of parotoid gland posteriorly to a point about two-thirds of the distance between axilla and groin; (10) hands and feet with long digits and reduced webbing; (11) subarticular tubercles present; (12) supernumerary tubercles present but poorly developed; (13) subdigital lamellar pads absent; (14) tensor fasciae latae not extended; (15) vocal slits absent; (16) cloacal sheath absent.

Description of holotype.—Snout-vent length (S-VL) 41.9 mm; tibia length 15.4 mm, 36.8 per cent of S-VL; foot length 23.3 mm, 55.6 per cent of S-VL; head length 14.7 mm, 35.1 per cent of S-VL; head width 16.4 mm, 39.1 per cent of S-VL; snout in dorsal aspect acuminate (Fig. 4a), in profile (Fig. 3a) long, directed anteroventrally, truncate terminally; distance from nostril to tip of snout equal to distance between nostril and eye, 3.3 mm, constituting 22.4 per cent of head length; tip of snout bulbous, connected by broad ventral keel to upper jaw; loreal region concave; nostrils protuberant, lateral, at level anterior to terminus of upper jaw, slightly ventral to canthal ridge; diameter of eye 4.0 mm, 27.2 per cent of the head length; pupil horizontally elliptical; interorbital distance 7.1 mm, 43.3 per cent of head width; ear absent; tongue twice as long as wide, widest at two-thirds its length, pointed anteriorly and posteriorly; tongue at greatest width about two-thirds as wide as mouth; posterior two-thirds of tongue free; choanae minute, round, lateral in position; prevomerine teeth and vocal slits absent.

Canthal ridges angular in section, converging anteriorly to form acuminate snout, terminating posteriorly in slight swellings at anterodorsal corner of orbit; crown of head with moderately developed, dorsally depressed cranial ridges; broad supraorbital ridge bordering medial edge of orbit, continuous with narrow postorbital crest; supratympanic crest continuous with postorbital ridge, narrow anteriorly, broad and depressed posteriorly adjacent to anterior margin of parotoid gland; occipital crest scarcely discernible spur produced at junction of supraorbital and postorbital ridges; pretympanic crest poorly-developed spur projecting ventrally from junction of postorbital and supratympanic ridges at posterior, dorsolateral margin of orbit.

Arms moderately robust and lacking folds; axillary membrane absent; fingers (Fig. 5a) long, slender; length of fingers from shortest to longest 1-2-4-3; phalangeal formula of hand 2-2-3-3; fingers vestigially webbed; subarticular tubercles of hand large but depressed; supernumerary tubercles of hand few and small in size; inner palmar tubercle round, flat; medial palmar tubercle large, one and one-half times as large as inner palmar tubercle, ovoid, less depressed than inner palmar tubercle; prepollical protuberance and nuptial excresence absent; hind limbs relatively long, lacking folds; toes long, slender (Fig. 6a); length of toes from shortest to longest 1-2-3-5-4, third and fifth about equal in length, phalangeal formula of foot 2-2-3-4-3; webbing extending to bases of penultimate phalanges of toes one and two; third toe one-half webbed; fourth toe one-fourth webbed; fifth toe one-half webbed; subarticular tubercles large, ovoid, depressed; supernumerary tubercles few in number, small, greatest proliferation between inner and out metatarsal tubercles; inner metatarsal tubercle large, flat, and irregularly shaped; out metatarsal tubercle round, slightly depressed, one-half size of inner metatarsal tubercle.

Cloacal opening directed posteroventrally at mid-level of thighs; no noticeable anal sheath; parotoid glands small, rounded in dorsal and lateral views; skin of dorsum with small, conical tubercles; scattered, indistinct, larger tubercles on eyelid, at angle of jaw and along flanks; skin of throat, chest, belly and posterior surfaces of thighs granular; dorsolateral row of small, rounded, depressed tubercles extending posteriorly from posterior margin of parotoid gland to a point about two-thirds distance between axilla and groin.

Dorsal ground color pale creamy tan with darker markings; reticulated dorsal dark brown marks forming interorbital bar with dark marks extending onto eyelids; V-shaped mark medial to each parotoid extending from occiput to posterior area of pectoral region; sacral area traversed by broad chevron; dorsal surface of limbs with narrow transverse bands proximally and wide transverse bands distally; hands and feet dark dorsally except for first and second fingers and first, second, and third toes which are marbled with creamy tan; flanks and postympanic areas predominately dark brown and grayish tan; belly and ventral surfaces of limbs creamy tan marbled with dark brown; palmar and plantar surface dark brown with grayish tan palmar and metatarsal tubercles; ventral ground color creamy tan with bold, dark brown marbling on limbs and belly; coalescence of marbling anteriorly to form nearly uniform dark brown throat region; scattered, small, white tubercles over entire venter.

Description and variation.—Eleven adult males from Cerro Malí and Cerro Tacarcuna, Panamá, have snout-vent lengths of 31.5 to 41.9 mm (mean 37.8 mm). Eight adult females from the same localities have snout-vent lengths of 40.6 to 49.1 mm (mean 44.9 mm). There is no marked intersexual or intrasexual variation in the measurements and ratios compared with those of the holotype.

In preservative, the dorsal ground coloration of *Rhamphophryne acrolopha* varies from a uniform dark brown to a medium or grayish brown. The former is less common; in these specimens the row of dorsolateral tubercles is grayish tan. There is an absence of any distinctive markings on the dorsal surfaces of the limbs or the side of the head. The posterior surfaces of the thighs and all ventral surfaces are heavily marbled with dark brown. Paler individuals are marked with a variety of dorsal spots and blotches ranging from gray to black in color. A partial or complete vertebral stripe and a light colored labial stripe may be present; occasionally, a mid-ventral stripe is present.

In life, dorsal colors have been observed to vary from yellowish tan to reddish and dark brown. The iris is bronze with black reticulations.

There is some variation among specimens in the development of cranial crests and the snout. In general, larger individuals, such as mature females, tend to have the most pronounced development of both crests and snout. This is to be expected as a result of continued ossification. In subadult specimens of *Rhamphophryne acrolopha,* the snout is more nearly truncate in profile; with increased size, the snout develops its typical anteroventral orientation.

Etymology.—The specific name is derived from the Greek *akrolophos* meaning crest of a mountain or ridge, with reference to the isolated occurrence of this species at high elevations in the Serranía del Darién.

Distribution.—Rhamphophryne acrolopha is known only from the Serranía del Darién (Cerro Tacarcuna and Cerro Malí) in Panamá and adjacent Colombia (Fig. 10).

Remarks.—Externally *Rhamphophryne acrolopha* most closely resembles, and most easily is confused with, *macrorhina* from Colombia. Both are relatively large members of the genus, and both are characterized by extremely protuberant snouts and small, depressed series of dorsolateral tubercles. It should be noted that the cranial crests and tubercles on the eyelids are more extensively developed in *macrorhina,* and the parotoid glands in that species are less evident than in *acrolopha.* The hands and feet are less specialized in *acrolopha* than in *macrorhina;* the tendency for formation of lamellar pads is less marked, webbing is comparatively reduced, and subarticular and supernumerary tubercles are more distinct in *acrolopha.* The inner and outer palmar tubercles are obvious in *acrolopha* but barely evident in *macrorhina.* Despite the external similarities of these species, they are quite distinct internally. *Rhamphophryne acrolopha* lacks vocal slits, whereas *macrorhina* retains them. Furthermore, *macrorhina* has eight presacral vertebrae and a weakly bicondylar sacral-coccygeal articulation in contrast to the seven presacral vertebrae and monocondylar articulation of *acrolopha.*

Virtually nothing is known concerning the habits and life history of this species. All specimens (adult males, females, and juveniles) were found by day amidst leaf litter on the forest floor between the months of January and July. The forest at the Cerro Malí site contains many small trees, including palms, reaching heights of about 12 m; larger trees, with heights to 30 m, are scattered throughout the forest. There is an understory of bushes and ferns, and most of the trees have a thick covering of moss on the trunks. The forest floor is characterized by a thick, mulch layer and many rotting logs. Bromeliads abound, but orchids and tree ferns are rare (Field notes, W. E. Duellman, July 10, 1963).

Gravid females were obtained during the months of February, March, and July. One female (KU 76964) from Cerro Malí contained a total of 145 unpigmented eggs on one side of the body cavity (eggs present on both sides of the body cavity for the species). Of this total, 50 of the eggs have an average diameter of 2.5 mm, whereas the remainder have diameters of less than 1.0 mm. Tadpoles are unknown.

Specimens examined.—(61) COLOMBIA: *Chocó:* East slope Cerro Malí, 1470 m, KU 76984, 76986, USNM 150941. PANAMA: *Darién:* Cerro Malí, 1265-1451 m, KU 76941 (juvenile), 76944 (juvenile), 76945, 76946-54 (juveniles), 76955-6 (skeletons), 76957-60 (juveniles), 76961-5, 76968-83 (juveniles), 76984, 76985-6 (juveniles), LACM 54337-8, MLS 1240, UMMZ 129694-5, USNM 151075-6; Cerro Tacarcuna, 1265-1481 m, USNM 151100 (juvenile), 151101, 151102-3 (juveniles), 151104-5, 151106 (skeleton), 151107; headwaters of Río Pucro, USNM 151071 (juvenile).

Rhamphophryne festae, new combination

Atelopus festae Peracca, 1904:18 [Syntypes.—IZS 2903 from Gualaquiza and 2904 from "Río Santiago" (= lower Río Zamora, *fide* Peters, 1955), Morona-Santiago Province, Ecuador; Enrico Festa, collector]. Noble, 1920:446. Peters, 1955:347.

Diagnosis.—A moderate-sized *Rhamphophryne* (♂ 42.0 mm, ♀ 45.8 mm) which can be distinguished from other members of the genus by the following combination of characters: (1) seven presacral vertebrae; (2) sacral vertebra fused with coccyx; (3) snout long, protuberant, directed anteroventrally; (4) cranial ornamentation moderately well developed; (5) supraorbital, postorbital, and supratympanic crests present; (6) pretympanic crest present; (7) occipital crest moderately developed; (8) dorsal tubercles scattered, minute, conical; (9) dorsolateral row of slightly enlarged, conical tubercles extending from posterior margin of skull to a point about three-fourths distance between axilla and groin; (10) hands and feet with some shortened digits and no marked reduction of webbing; (11) subarticular tubercles present; (12) supernumerary tubercles present; (13) subdigital lamellar pads absent; (14) tensor fasciae latae extended; (15) vocal slits absent; (16) cloacal sheath absent.

Description and variation.—Average measurements of three adult females and three adult male *Rhamphophryne festae* are, as follows (corresponding figures for males are included in parentheses after females): snout-vent length (S-VL) 37.2 mm (33.2 mm); tibia 12.1 mm (10.9 mm), 31.9 (33.4) percent of S-VL; foot and tarsus length 17.1 mm (15.8 mm), 46.6 (48.2) per cent of S-VL; head length 12.7 mm (11.3 mm), 34.0 (34.2) per cent of S-VL; head width 13.6 mm (12.6 mm), 38.2 (38.1) per cent of S-VL. The snout in dorsal aspect (Fig. 4b) is acuminate, and in profile (Fig. 3b) is moderately long, directed anteroventrally, and acuminate terminally. The distance from the nostril to the tip of the snout (♀ 2.3 mm, of ♂ 2.1 mm) is noticeably less than the distance from the nostril to the eye (♀ 2.9 mm, ♂ 2.6 mm). The tip of the snout is pointed, not bulbous, and a sharp, ventral keel runs from the tip of the snout to the upper jaw. The loreal region is concave. Nostrils are slightly protuberant and lateral; they are located at a level anterior to the terminus of the upper jaw and ventral to the canthal ridge. The diameter of the eye is 3.7 mm (3.3 mm), 29.9 (29.6) per cent of the head length. The pupil is horizontally elliptical. The interorbital distance is 6.1 mm (5.9 mm), 44.9 (46.8) per cent of the head width. The ear is absent. The tongue is small, pointed anteriorly and round posteriorly. It is three-fourths as wide as long, widest at one-half its length, and slightly more than one-third as wide as the mouth. The posterior half of the tongue is free. Choanae are minute, round, and lateral in position. Prevomerine teeth are absent.

The canthal ridges are angular in section and converge anteriorly to form the acuminate snout. Cranial ridges are present and moderately well developed in larger individuals (Fig. 4b). The supraorbital, postorbital and supratympanic crests are narrow; in smaller specimens, they bear series of small, conical tubercles throughout their lengths. The pretympanic crest does not bear tubercles. The occipital crest is absent in smaller individuals (Fig. 11b); in place of the crest, there is a row of small tubercles. Larger individuals have a moderately well-developed occipital crest which is most obvious near its junction with the supraorbital and postorbital cranial crests.

The arms are slender and lack folds. An axillary membrane is absent. Some of the fingers are reduced in length (Fig. 5b), their lengths from shortest to longest being 2-4-1-3. The phalangeal formula of the hand is 2-2-3-3. Webbing extends to the bases of the penultimate phalanges of fingers one, two, and four. The third finger is basally webbed. The inner palmar tubercle is moderate in size, elliptical and flat. Supernumerary and subarticular tubercles are present. The medial palmar tubercle is twice as large as the inner tubercle, ovoid, and flat. Males lack prepollical protuberances and nuptial excrescences. The hind limbs are relatively long, slender, and lack folds. Some of the toes are reduced in length, their lengths from shortest to longest being 1-2-3-5-4; the third and the fifth toes are about equal in length (Fig. 6b). The phalangeal formula of the foot is 2-2-3-4-3. Webbing extends to the bases of the penultimate phalanges of all toes except the fourth which is webbed basally. Subarticular and supernumerary tubercles are present. The inner metatarsal tubercle is moderate in size, irregularly shaped and flat, whereas the outer metatarsal tubercle is small (one-half the size of the inner metatarsal tubercle), ovoid and depressed.

The cloacal opening is directed posteriorly at the upper level of the thighs. A cloacal sheath is absent. The parotoid glands are moderately well developed in larger specimens; however, in smaller specimens they are small, barely evident dorsally, and most obvious in lateral view as long, narrow swellings ventral to the dorsolateral tubercle row (Fig. 11a and b). There is a proliferation of minute, conical tubercles scattered over the dorsal surfaces of the body; these tubercles are especially concentrated on the dorsal surfaces of the limbs. Small tubercles cover the eyelids and line the cranial ridges. A series of very slightly enlarged tubercles runs in a posterodorsal direction from the angle of the jaw, and dorsolaterally from the posterior margin of

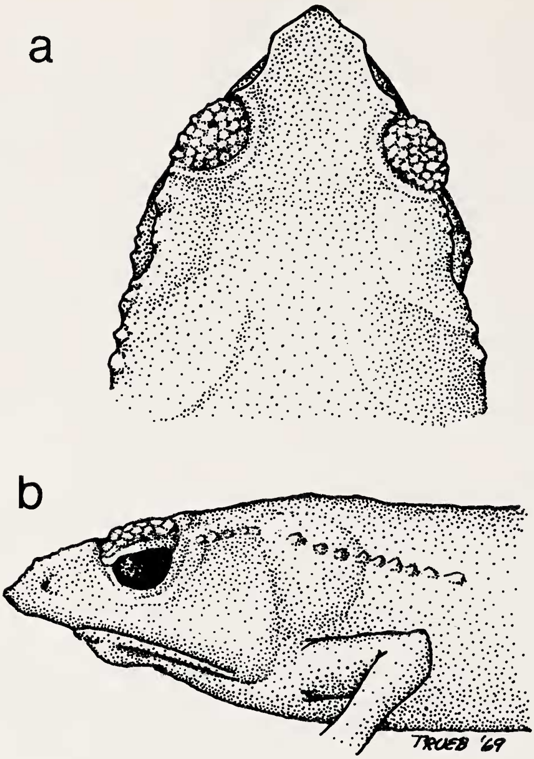

FIGURE 11. Immature *Rhamphophryne festae,* ♂, 26.5 mm snout-vent length (USNM 167175): (a) dorsal; (b) lateral. × 3.

the supratympanic ridge, posteriorly, to a point about three-fourths of the distance between the axilla and the groin. The skin of the throat, chest, belly, flanks, ventral surfaces of the limbs, and the anterior and posterior surfaces of the thighs is granular.

In preservative, the dorsal ground color of *Rhamphophryne festae* varies from a uniform dark brown to yellowish tan. Darker mottling and transverse bars are evident on paler specimens. The ventral surfaces vary from yellowish tan to dark brown in color. In some, the venters are uniform, whereas in others, they are variously mottled with dark brown. The palmar and plantar tubercles and digital pads of all specimens are creamy tan in color.

Rhamphophryne festae, in life, is reddish brown above with slightly darker cross-banding, according to color notes recorded by James A. Peters (personal communication). The tubercles forming the dorsolateral tubercle row have orange-red heads. The belly is a dull, dusty red with bluish white mottling posteriorly. The venters of the digits are pale pink, and the iris is black with a narrow ring of gold surrounding the pupil.

Distribution.—*Rhamphophryne festae* is known from moderate and low elevations (100-700 m) on the Atlantic Andean slopes and upper Amazon Basin of Ecuador (Fig. 10).

Remarks.—Although one of the syntypes (IZS 2903) of *Rhamphophryne festae* is a gravid female, it lacks certain diagnostic features evident on larger, more mature specimens (compare Figs. 3b, 4b, and 11). The cranial crests are much more evident on the larger specimens and the snout more protuberant. The hands and feet, and other characteristics described by Peracca (1904) are virtually the same.

Rhamphophryne festae is possibly the most specialized member of the genus. The highly modified feet render *festae* readily distinguishable from other species of *Rhamphophryne*. The triangular head and the physiognomy of the hands and feet are probably responsible for the original placement of this species in the genus *Atelopus*; it should be noted that the cervical and first presacral vertebrae are not fused in *festae*, whereas these elements are characteristically fused in all *Atelopus*.

The specialization of *Rhamphophryne festae* is most evident internally. *Rhamphophryne rostrata* and *festae* are the only two members of the genus having a fused coccyx and sacrum, which presumably is an advancement over the weakly bicondylar articulation of *macrorhina*. Like *acrolopha*, and in contrast to *rostrata, nicefori,* and *macrorhina, festae* has lost the vocal slits. The second and fourth fingers and the first, second, third and fifth toes are notably short; the phalangeal formulae are normal, although the individual phalangeal elements of the digits are shortened and poorly, if at all, ossified.

Very little natural history information is available. Peters observed that a subadult specimen obtained in July was found on a log in the jungle, quite high above any of the streams. A gravid female (USNM 167174) contains relatively few, large (1.8 mm), unpigmented eggs.

Specimens examined.—(18) ECUADOR: *Napo*: near Arajuno, 537 m, KU 124949-50, USNM 167176; Loreto, CAS 11414-7, USNM 167175; *Pastaza*: Alto Río Pucayacu, USNM 167168 (skeleton), 167169; Don Tomás, 5 km S Montalvo, USNM 167172; Río Bobonaza, 703 m, USNM 167167; Río Solis (headwaters), USNM 167174; Río Capahuari (headwaters), USNM 167171; Río Rutuno (tributary of Río Bobonaza), USNM 167170; Río Villano USNM 167173; *Morona-Santiago*: Gualaquiza, IZS 2903; "Río Santiago" (= lower Río Zamora, *fide* Peters, 1955), IZS 2904.

Rhamphophryne macrorhina, new species

Bufo rostratus (part) Noble, 1920:445. Gallardo, 1962:96. Cochran and Goin, 1970:93.

Holotype.—Adult female, Los Angeles County Museum of Natural History (LACM) 44394 from Santa Rita, Departamento de Antioquia, Colombia, between elevations of 1890 and 1910 m, one of a series obtained on June 9, 1968, by P. A. Silverstone and J. Ramos.

Paratypes: LACM 44395 and KU 124946 obtained with the type by P. A. Silverstone and J. Ramos; KU 124947 (skeleton) from the type locality at an elevation of 1930 m on June 8, 1968, by P. A. Silverstone and J. Ramos.

Diagnosis.—A large *Rhamphophryne* (♂ 43.4 mm, ♀ 51.0 mm) which can be distinguished from other members of the genus by the following combination of characters: (1) eight presacral vertebrae; (2) sacral vertebra not fused with coccyx, with a weakly bicondylar articulation; (3) snout long, protuberant, and directed anteroventrally; (4) cranial ornamentation well developed; (5) supraorbital, postorbital, and supratympanic crests present; (6) pretympanic crest present; (7) occipital crest present and distinct; (8) dorsal tubercles scattered, small and rounded; (9) dorsolateral row of small, depressed tubercles extending from posterior margin of parotoid gland posteriorly to a point about one-half distance between axilla and groin; (10) hands and feet with moderate-sized digits and no marked reduction of webbing; (11) subarticular tubercles absent; (12) supernumerary tubercles present; (13) tendency towards presence of subdigital lamellar pads; (14) tensor fasciae latae not extended; (15) vocal slits present in males; (16) cloacal sheath absent.

Description of holotype.—Snout-vent length (S-VL) 51.4 mm; tibia 16.0 mm, 31.1 per cent of S-VL; foot length 26.0 mm, 50.6 per cent of S-VL; head length 18.2 mm, 35.4 per cent of S-VL; head width 18.8 mm, 36.6 per cent of S-VL; snout in dorsal aspect (Fig. 4c) acuminate, in profile (Fig. 3c) long, directed anteroventrally, acuminate terminally; distance from nostril to tip of snout about equal to distance between nostril and eye, 4.0 mm, constituting 22 per cent of head length; tip of snout bulbous, not connected by distinct ventral keel to upper jaw; loreal region concave; nostrils slightly protuberant, lateral, at level anterior to terminus of upper jaw, ventral to canthal ridge; diameter of eye 4.8 mm, 26.4 per cent of head length; pupil horizontally elliptical; interorbital distance 8.2 mm, 43.6 per cent of head width; ear absent; tongue slightly less than twice as long as wide, widest at one-half its length, pointed anteriorly, rounded posteriorly; tongue at greatest width about one-half as wide as mouth; posterior five-eighths of tongue free; choanae minute, round, lateral in position; prevomerine teeth absent; vocal slits present in males.

Canthal ridges angular in section, converging anteriorly to form acuminate snout (Figs. 3c and 4c), terminating posteriorly in slight swelling at anterodorsal corner of orbit; crown of head with well-developed cranial ridges; distinct supraorbital ridge bordering medial edge of orbit, continuous with well-developed postorbital crest; supratympanic crest continuous with postorbital ridge, narrow anteriorly, expanded posteriorly and depressed posteromedially; posteromedial portion of supraorbital crest bordering anterior margin of parotoid gland; occipital crest well-developed ridge, produced at junction of supraorbital and postorbital crests; pretympanic crest moderately well-developed spur projecting ventrally from union of postorbital and supratympanic ridges at posterior, dorsolateral margin of orbit.

Arms moderately slender and lacking folds; axillary membrane absent; fingers of moderate length, not especially slender (Fig. 5c); length of fingers from shortest to longest 2-1-4-3, first and third about equal in length; phalangeal formula of hand 2-2-3-3; webbing extending from ultimate phalange of first finger to distal part of penultimate phalange of second finger, from base of ultimate phalange of second finger to base of antepenultimate phalange of third finger, from base of antepenultimate of third finger to base of penultimate of fourth finger; subarticular tubercles absent; series of subdigital, lamellar, pad-like swellings on each finger; supernumerary tubercles scattered, few in number; inner palmar tubercle absent; medial palmar tubercle ovoid, depressed, indistinct; hind limbs relatively long, lacking folds; toes of moderate length, not especially slender (Fig. 6c); length of toes from shortest to longest 1-2-3-5-4, third and fifth about equal in length; phalangeal formula of foot 2-2-3-4-3; first two toes fully webbed; second and fifth toes three-fourths webbed; third toe about one-third webbed; subarticular tubercles absent; series of subdigital, lamellar, pad-like swellings on each toe; supernumerary tubercles scattered principally on central plantar surface; inner metatarsal tubercle elliptical, flattened; outer metatarsal tubercle about two-thirds size of inner metatarsal tubercle, ovoid, depressed.

Cloacal opening directed posteriorly at mid-level of thighs; cloacal sheath absent; parotoid glands small, indistinct, and diffuse dorsally, scarcely evident laterally; skin of dorsum with a few scattered, depressed tubercles; round, densely distributed tubercles covering eyelid; three larger, conical tubercles arranged in posterodorsally oriented row at angle of jaw; other conical tubercles on limbs and around anus; skin of throat, chest, belly and posterior surfaces of thighs granular; dorsolateral row of small, rounded, depressed tubercles extending posteriorly from posterior margin of parotoid gland to about mid-point of distance between axilla and groin.

Dorsal ground color medium brown; indistinct and variable creamy tan mottling on back and first two digits of hand and foot; delicate, incomplete vertebral line on posterior one-third of dorsum; dorsolateral tubercle row grayish tan; flanks and sides of head mottled brown; limbs dark brown dorsally with light colored tubercles along lateral edges; distinct, pale, creamy tan area anterior to forelimb and at angle of jaw on upper lip; less distinct pale spot ventral to eye; venter yellowish tan delicately mottled with dark brown; concentrations of darker pigment around mandible and in gular and pectoral regions; scattered, cream colored tubercles on venter, most numerous at angle of jaw and in pectoral region.

Description and variation.—Four adult males have snout-vent lengths of 35.6, 42.1, 43.4, and 43.7 mm (mean 41.2 mm). All measurements and ratios are comparable to those of the holotype except one. The interorbital distance of the four males is 45.3 per cent (42.9-52.9) of the head width, whereas the interorbital distance of the female is only 43.6 per cent of the head width. Interorbital distances were measured between the medial margins of the supraorbital crests, thus the apparent variation probably only reflects the greatly thickened condition of the crests in the large female. Similarly, the other cranial crests are less well developed and the snouts straighter in the smaller and less extensively ossified males, females, and the single juvenile specimen.

In preservative, the only color variation noted is in the dorsal marking. The males tend to have distinct creamy tan dorsal spots which are absent on the large female. In life, a subadult female (LACM 44393) was noted to be dull, dark brown above and light brown marbled with dark brown below; there were some traces of ruddy on the venter and sides. The iris was yellow, heavily reticulated with black and with a ring of bright yellow around the pupil. A horizontal, brown line divided the iris. Limbs were dull buff ventrally, marbled with brown.

Etymology.—The specific name is derived from the Greek prefix *macro*, meaning large, and the Greek word *rhinos*, meaning nose, with reference to the inordinately long snout of this species.

Distribution.—Rhamphophryne macrorhina is known only from four localities in Colombia (Fig. 10). It has been obtained at Santa Rita north of Medellín, at localities 6 km ESE of Villa María and 8 km S Valdivia, and from Santa Rita Creek, 14 miles N of the village of Mesopotamia (south of Medellín). There is some question as to the validity of the latter locality. Santa Rita lies to the east of Mesopotamia, rather than to the north, according to Richard Newcomer (Stephen R. Edwards, personal communication).

Remarks.—Rhamphophryne macrorhina is superficially most similar to *R. acrolopha*; for a comparison of these two species, refer to the remarks section in the account of *acrolopha*. Morphologically, *macrorhina* combines highly specialized external characters with some of the least specialized internal characters found in the genus. The tendency toward shortened digits, formation of subdigital lamellar pads, reduction of palmar tuberculation and parotid glands, and proliferation of cranial crests obviously represent derived character states. In contrast to the latter, *macrorhina* is the only member of *Rhamphophryne* which retains eight presacral vertebrae. The sacral-coccygeal articulation is very weakly bicondylar, that is, the separation between the sacral condyles is reduced to a shallow groove. This condition seems to be a modification of the bicondylar articulation characteristic of most other bufonids.

Cochran and Goin's (1970) redescription of *Bufo rostratus* was based on a specimen of *Rhamphophryne macrorhina* (AMNH 1384, a paratype of *Bufo rostratus*). The specimen redescribed is a male, not a female as stated. The dorsolateral tubercles are not conical, but depressed. The upper jaw does not extend beyond the lower jaw, although the anterior position of the nostrils might create this illusion. The tympanum is not hidden; it is absent.

P. A. Silverstone (personal communication) collected four individuals (an adult male, subadult and gravid female, and a juvenile) of *Rhamphophryne macrorhina* in June. Each was obtained by day on the ground of a forested hillside not close to any body of water. Although males were not observed to call, one individual (a young female) uttered a "sad, small squeak" when handled. Noble (1917) provided a description of the habitat in which one individual was found (refer to the remarks section in the account of *Rhamphophryne rostrata*).

A gravid female has relatively few, large (about 2 mm), unpigmented eggs. Males lack prepollical protuberances and nuptial excrescences.

Specimens examined: (9) COLOMBIA: *Antioquia:* Santa Rita, 1890-1910 m, KU 124946, 124947 (skeleton), LACM 44394-5; Santa Rita Creek, 14 miles N Mesopotamia, 1890-2424 m, AMNH 1384; 8 km S. Valdivia, 1450 m, FMNH 63838-40; *Caldas:* 6 km ESE Villa María, 2130 m, KU 129904.

Rhamphophryne nicefori, new combination

Bufo rostratus nicefori Cochran and Goin, 1970:95 [Holotype.—USNM 163476 from Hacienda Palmas, El Chaquiro, Departamento de Antioquia, Colombia, elevation 2670 m; obtained in December, 1966, by Hno. Nicéforo María].

Diagnosis.—A small species of *Rhamphophryne* (♂ 32 mm, ♀ 33 mm) which can be distinguished from other members of the genus by the following combination of characters: (1) seven presacral vertebrae; (2) sacral vertebra not fused with coccyx, with a monocondylar articulation; (3) snout moderately short, protuberant and directed slightly anteroventrally; (4) cranial ornamentation evident; (5) supraorbital crest present and postorbital and supratympanic crests absent; (6) pretympanic crest barely evident; (7) occipital crest present; (8) dorsal tubercles scattered, large, depressed; (9) dorsolateral row of enlarged, depressed tubercles extending from posterior margin of parotoid gland to a point about three-fourths the distance between the axilla and groin; (10) hands and feet with relatively short, heavy digits and reduced webbing; (11) subarticular tubercles absent; (12) supernumerary tubercles present; (13) subdigital lamellar pads present; (14) tensor fasciae latae extended; (15) vocal slits present in males; (16) cloacal sheath present.

Description and variation.—Average measurements of two adult female and measurements of one adult male *Rhamphophryne nicefori* are as follows (corresponding figures for male are included in parentheses after females): snout-vent length (S-VL) 32.9 mm (31.9 mm); tibia length 9.0 mm (10.2 mm), 29.1 (32.0) per cent of S-VL; foot length 16.1 mm (15.0 mm), 48.8 (47.0) per cent of S-VL; head length 10.1 mm (10.0 mm), 30.7 (31.3) per cent of S-VL; head width 11.4 mm (11.1 mm), 34.5 (34.8) per cent of S-VL. The snout in profile (Fig. 3d) is moderately short, directed slightly anteroventrally, and rounded terminally and in dorsal aspect (Fig. 4d) is acuminate. The distance from the nostril to the tip of the snout (♀ 1.7 mm, ♂ 1.9 mm) is equal to or less than the distance from the nostril to the eye (♀ 2.2

mm, ♂ 1.9 mm). The tip of the snout is rounded; there is no evidence of a ventral keel connecting the tip to the upper jaw. The loreal region is concave. Nostrils are slightly protuberant and lateral; they are located at a level obviously posterior to the terminus of the upper jaw and ventral to the canthal ridge. The diameter of the eye is 3.2 mm (3.3 mm), 31.7 (33.0) per cent of the head length. The pupil is horizontally elliptical. The interorbital distance is 4.0 mm (4.0 mm), 34.9 (36.0) per cent of the head width. The ear is absent. The tongue is pointed anteriorly and round posteriorly. It is one-half as wide as long, widest at two-thirds its length, and at its widest point, about one-half as wide as the mouth. The posterior one-third of the tongue is free. Choanae are small, round and lateral in position. Prevomerine teeth are absent. Vocal slits are present in males.

The canthal ridges are angular in section and converge anteriorly to form the acuminate snout. Some of the cranial ridges are obvious. The supratympanic and occipital crests are very well developed. The postorbital crest is absent. The presence of a supratympanic crest is questionable; in preserved specimens this area is obscured by an anterolateral, finger-like projection of the parotoid gland. However, a skeletal preparation might reveal the presence of a small supratympanic ridge.

The arms are robust and lack folds. An axillary membrane is absent. The fingers are short and thick (Fig. 5d); their lengths from shortest to longest being 1-2-4-3; the phalangeal formula of the hand is 2-2-3-3. The fingers are about one-fourth, or less, webbed. Supernumerary tubercles are present. Subarticular tubercles are absent; instead, the digits bear lamellar, pad-like swellings. Males apparently lack prepollical protuberances and nuptial excrescences. The inner palmar tubercle is indistinct or absent in females; in males it is distinct and ovoid. The medial palmar tubercle is round and in the male, about the same size as the inner tubercle. The hind limbs are short, robust and lack folds. The toes are short and thick (Fig. 6d), their lengths from shortest to longest being 1-2-3-5-4; the phalangeal formula of the foot is 2-2-3-4-3. The first three toes are about three-fourths webbed. The fourth and fifth toes are one-third webbed. A few supernumerary tubercles are present. Subarticular tubercles are absent; the toes bear subdigital, lamellar, pad-like swellings. The inner metatarsal tubercle is ovoid, depressed, and variously indistinct or distinct depending on the specimen. The outer metatarsal tubercle, if present, is round and indistinct. It often is absent.

The cloacal opening is directed posteroventrally at the mid-level of the thighs. A relatively long cloacal sheath is present. The parotoid glands are large, rounded and obvious both dorsally and laterally. An anterior, dorsolateral extension of the parotoid gland extends from the main body of the gland to the corner of the eye. Scattered, depressed tubercles occur over the dorsum; these are densely distributed on the limbs and the flanks. Small, round tubercles cover the eyelids. A dorsolateral series of larger, depressed tubercles extends posteriorly from the parotoid gland to a point about three-fourths the distance between the axilla and the groin; occasionally, adjacent tubercles coalesce to form a long, irregularly shaped swelling. The entire skin is rather coarsely granular.

In preservative, both females are uniform dark brown above and slightly lighter brown below with no visible markings. The male has a dark brown dorsal ground color, and a tan vertebral stripe; all dorsal surfaces are marked with a fine reticulate network of light tan. The ventral surfaces are light brown in color, marbled with a slighly darker brown. There is an indication of an incomplete mid-ventral stripe. The subadult female and the juvenile specimens are marked similarly to the adult male, except that the dorsal light markings are more extensive. There is no information available on the colors in life.

Distribution.—Rhamphophryne nicefori is known only from the type locality at Hacienda Palmas, El Chaquiro, Departamento de Antioquia, Colombia (Fig. 10).

Remarks.—Rhamphophryne nicefori is intermediate in terms of specialization and characters shared with other members of the genus. Development of cranial crests is less obvious than in *acrolopha* and *macrorhina,* and more obvious than in *rostrata* and *festae.* The presence of relatively large, widely spaced conical tubercles and a less protuberant snout relates *nicefori* with *rostrata.* Like *acrolopha, nicefori* has a monocondylar sacral-coccygeal articulation, but the hands and feet are most similar to *macrorhina.* The digits are relatively short and there is a tendency toward formation of subdigital, lamellar pads; palmar and metatarsal tubercles are much less evident in *nicefori* than in *macrorhina.*

During the month of December, three females (two adults and one young), an adult male, and a juvenile were collected by day. The gravid female contains relatively few, large (1.8 mm), unpigmented eggs.

Specimens examined.—(5) COLOMBIA: *Antioquia:* El chaquiro, Hacienda Palmas, 2760 m, KU 124948, MLS 449, 451-2, USNM 163476.

Rhamphophryne rostrata, new combination

Bufo rostratus (part) Noble, 1920:445 [Holotype.—American Museum of Natural History (AMNH) 1359 from Santa Rita Creek, 14 miles north of the village of Mesopotamia in the Department of Antioquia, Colombia; R. D. O. Johnson, collector]. Gallardo, 1962:96. Cochran and Goin, 1970:93.

Diagnosis.—A large *Rhamphophryne* (♂ 42 mm) which can be distinguished from other members of the genus by the following combination of characters: (1) seven presacral vertebrae; (2) sacral vertebra fused with coccyx; (3) snout moderately long, protuberant, not directed posteroventrally; (4) cranial ornamentation scarcely evident; (5) supraorbital and postorbital crests absent, and supratympanic crest present; (6) pretympanic crest present; (7) occipital crest absent; (8) dorsal tubercles scattered, large, rounded; (9) dorsolateral row of seven large tubercles extending between posterior margin of parotoid gland and groin; (10) hands and feet with long, slender digits, and no marked reduction of webbing; (11) subarticular tubercles present; (12) supernumerary tubercles present; (13) subdigital lamellar pads absent; (14) tensor fasciae latae not extended; (15) vocal slits present in males; (16) cloacal sheath absent.

Description.—Rhamphophryne rostrata is known only from two specimens, the holotype, an adult male (AMNH 1359; Fig. 2), and a juvenile (AMNH 1362). Measurements of the holotype are as follows: snout-vent length (S-VL) 42.0 mm; tibia 15.3 mm, 36.4 per cent of S-VL; foot length 25.1 mm, 59.8 per cent of S-VL; head length 13.6 mm, 32.4 per cent of S-VL; head width 14.3 mm, 39.1 per cent of S-VL. The snout in dorsal aspect (Fig. 4e) is acuminate, and in profile (Fig. 3e) is moderately long, straight, and slightly rounded terminally. The distance from the nostril to the tip of the snout (2.4 mm) is noticeably less than the distance from the nostril to the eye (3.3 mm). The tip of the snout is not bulbous; a sharp ventral keel runs from the tip of the snout to the upper jaw. The loreal region is concave. Nostrils are slightly protuberant and lateral; they are located at a level anterior to the terminus of the upper jaw and ventral to the canthal ridge. The diameter of the eye is 4.6 mm, 33.8 per cent of the head length. The pupil is horizontally elliptical. The interorbital distance is 6.5 mm, 45.5 per cent of the head width. The ear is absent. The tongue is slightly less than twice as long as wide; it is widest at one-half its length, pointed anteriorly, and rounded posteriorly. The tongue is one-half as wide as the mouth and free posteriorly for one-fourth of its length.Choanae are minute, round and lateral in position. Prevomerine teeth are absent. Vocal slits are present in males.

The canthal ridges are angular in section and converge anteriorly to form the acuminate snout. Cranial ridges are scarcely evident on the crown of the head. Supraorbital, occipital, and postorbital crests are absent. Supratympanic and pretympanic crests are obvious in lateral view.

The arms are moderately slender and lack folds. An axillary membrane is absent. The fingers are long and slender (Fig. 5e), their lengths from shortest to longest being 1-2-4-3; the phalangeal formula of the hand is 2-2-3-3. The first and second fingers are one-half webbed, whereas the third and fourth are only about one-fourth webbed. Supernumerary and subarticular tubercles are present. The inner palmar tubercle is elliptical, flat and indistinct, whereas the medial palmar tubercle is larger, round and distinct. The hind limbs are relatively long and lack folds. The toes are long and slender (Fig. 6e), their lengths from shortest to longest being 1-2-3-5-4; the phalangeal formula of the foot is 2-2-3-4-3. The first toe is fully webbed. Webbing extends from the ultimate phalange of the second toe to the base of the penultimate phalange of the third, from the base of the ultimate phalange of the third toe to the base of the antepenultimate phalange of the fourth, and from the base of the antepenultimate phalange of the fourth toe to the base of the penultimate phalange of the fifth toe. Supernumerary and subarticular tubercles are present. The inner metatarsal tubercle is moderate-sized, elliptical and flat, whereas the outer metatarsal tubercle is round, flat, and only about one-half the size of the inner metatarsal tubercle.

The cloacal opening is directed posteriorly at the mid-level of the thighs. An cloacal sheath is absent. The parotoid glands are relatively large and distinct, especially in lateral view. The dorsal surfaces of *Rhamphophryne rostrata* have scattered, large tubercles which are rather densely distributed on the limbs. The eyelids are covered with many smaller, round tubercles. Dorsolaterally there is a series of seven, enlarged tubercles between the posterior margin of the parotoid gland and the groin. Groups of other large tubercles occur at the angle of the jaw laterally and ventrally. The skin of the throat, chest, belly and posterior surfaces of the thighs is slightly granular.

The two specimens of *Rhamphophryne rostrata* are badly faded. In preservative, both are an almost uniform light brown color. The holotype appears to have had some darker brown mottling dorsally on the anterior and dorsal surfaces of the thighs, the flanks, and laterally, anterior to the forearm. There is a faint indication of darker transverse bars on the distal parts of the limbs. Ventrally, the belly, chest and throat are light brown with indistinct traces of delicate, darker brown mottling.

Distribution.—Rhamphophryne rostrata is known only from the type locality 14 miles N of Mesopotamia, Departamento de Antioquia, Colombia (Fig. 10). For remarks about this locality, refer to the section on distribution in the *R. macrorhina* account.

Remarks.—The relationships of *Rhamphophryne rostrata* are especially confusing because this species is represented by only one adult specimen, a male in a relatively poor state of preservation. Until a gravid female is available, it is impossible to ascertain the nature of the eggs. However, on the bases of the other morphological evidence, it seems reasonable to assume, at least for the present, that *rostrata* probably has large, unpigmented eggs. Externally, *rostrata* is the least specialized member of the genus. Cranial crests are absent, dorsal tubercles are scattered, hands and feet are generalized and the snout protrudes anteriorly only slightly. In contrast, internally, there are only seven presacral vertebrae and the sacrum is fused to the coccyx. Contrary to Noble's (1920) description, the tympanum is absent, not hidden.

Some information on the habitat of *Rhamphophryne rostrata* and *R. macrorhina* is available from a letter of Mr. R. D. O. Johnson quoted in part by Noble (1917). According to Johnson, the area of the type locality is cool (daytime temperature 58-68°F.), shaded, and moist. Ferns and mosses are common, and the forest floor is covered with a mass of decaying leaves, mosses and ferns, all held together by fine roots. This ground cover is locally termed "capote."

Specimens examined.—(2) COLOMBIA: *Antioquia:* Santa Rita Creek, 14 miles N Mesopotamia, 1890-2424 m, AMNH 1359, 1362 (juvenile).

INTRAGENERIC RELATIONSHIPS

Unfortunately the morphological features characterizing the species of *Rhamphophryne* are not especially suggestive of evolutionary trends and phylogenetic relationships within the genus. If one can assume that the genus has been derived from a more generalized bufonid stock such as the *Bufo valliceps* line (Tihen, 1962), then the following evolutionary trends can be postulated. There is a tendency towards reduced ossification and reduction in the number of osteological elements. Some of these alterations might be associated with the relatively small sizes of the species and their inclination towards a walking rather than a hopping gait. The length of the limb bones are obviously shortened in comparison with those of a typical *Bufo*. The pectoral girdle, although arciferal, is modified slightly in the direction of firmisterny. The vertebral column tends to be shortened by a reduction in the number of presacral vertebrae. It would seem reasonable to assume that the replacement of a bicondylar sacral-coccygeal articulation with a monocondylar articulation would result in some loss of axial stability. Fusion of the sacrum and coccyx overcomes inherent stability problems at the expense of mobility and axial flexibility posteriorly. Although the three structural conditions, i.e. weak bicondyly, monocondyly and fusion seem to constitute a natural evolutionary sequence, monocondyly and fusion may actually represent two divergent structural adaptations.

Cranial structure cannot be unequivocally categorized as being either one of reduced ossification (and therefore, by implication, "advanced" or "specialized") or not markedly reduced ossification ("generalized"). It has become increasingly evident from recent studies on modern anurans (Trueb, 1970) that trends towards loss of elements and reduced ossification in some parts of a frog skull may be countered by increased ossification and/or the development of additional structural elements elsewhere in the skull. Present evidence suggests that cranial restructuring by increased ossification reflects structural adaptations imposed on a more general evolutionary trend towards reduced ossification. The cranial structure of species of *Rhamphophryne* has obvious marks of reduction in the loss of complete integumentary-cranial co-ossification, loss of the ear apparatus, and reduced size of the prevomers. In contrast, there have been marked alterations in the anterior end of the skull involving proliferation of the sphenethmoid bone to produce the protuberant snout characteristic of this genus. The characteristic is least developed in *rostrata* and *nicefori*, and maximally developed in *festae* and *macrorhina*. A structural alteration of this kind, involving modification of an endochondral structure, would seem to represent a single evolutionary trend.

Characteristics of the soft anatomy are often more plastic and therefore more difficult to interpret than osteological features. In *Rhamphophryne* there is a tendency towards loss of vocal slits (the slits are absent in *festae* and *acrolopha* and present in the other species) which can be logically correlated with the absence of ears. Several trends seem to be evident in the structure of the hands and feet. There is a tendency towards marked shortening of the digits and reduction of webbing in *festae, macrorhina,* and especially *nicefori.* All of the digits are shortened in *macrorhina* and *nicefori,* whereas in *festae* the third finger and fourth toe remain long in comparison with the other digits. The digits are longer and more slender in *rostrata* and *acrolopha;* webbing is somewhat reduced in *acrolopha,* but not notably so in *rostrata.* Patterns of palmar and plantar tuberculation seem to be expressed in two general ways. *Rhamphophryne rostrata, festae,* and *acrolopha* have well-developed palmar, metatarsal, and subarticular and supernumerary tubercles typical of the more generalized bufonids. *Rhamphophryne macrorhina* and *nicefori* have less distinct palmar and supernumerary tubercles, and the subarticular tubercles have been replaced by subdigital, lamellarlike pads. Consideration of these trends suggests that there have been at least two evolutionary lines within the genus with respect to hand and foot morphology. That of *rostrata* and *acrolopha* seems to be more generalized and presumably representative of an ancestral type from which the other's could have arisen. The hands and feet of *festae* are so obviously different from those of *macrorhina* and *nicefori* that it would seem that two separate structural adaptations have appeared among these three species.

A summary of the individual characters possessed by each species would show that many of the proposed evolutionary trends overlap and contradict one another. As an example, on the bases of cranial and external morphology, *rostrata* seems to be the most generalized member of the genus. However, the presence of only seven presacral vertebrae and a fused coccyx and sacrum confuse the picture. *Rhamphophryne macrorhina,* on the other hand, appears to be quite specialized on the basis of external features; it is the only member of the genus having eight presacral vertebrae and a weak, but nonetheless bicondylar sacral-coccygeal articulation.

It is obvious that if any intrageneric relationships are to be postulated on the bases of the present, limited amounts of evidence, equivalent consideration cannot be given to all characters. The most conservative characters available for interpretation are those involving the osteology. On this basis I would propose that *rostrata* and *macrorhina* most closely resemble the ancestral stock of the genus, as evidenced by the condition of the sphenethmoid in the former and the vertebral column in the latter. This hypothesis is corroborated by the generalized morphology of the hands and feet and the retention of vocal slits in these species. The generalized condition (i.e. with respect to other bufonids) of the vertebral column of *macrorhina* seems to suggest that it may be an early derivative of an evolutionary line which gave rise to the three remaining species by a reduction in the number of presacral vertebrae from eight to seven. Of these three species, *nicefori* and *acrolopha* seem to constitute one evolutionary line relatively closely related to *macrorhina; festae* represents a second, more divergent line. *Rhamphophryne acrolopha* and *nicefori* are alike in having a monocondylar sacral-coccygeal articulation and similarly modified hands and feet. Of the two species, *nicefori* is somewhat less specialized in retaining vocal slits and lacking the protuberant snout characteristic of *acrolopha. Rhamphophryne festae* is probably the most specialized and divergent member of the genus. It lacks vocal slits, has a highly modified cranial structure, seven presacral vertebrae and a fused sacrum and coccyx. The hands and feet are specialized and dissimilar from any other member of the genus.

The nature of the diagnostic characters distinguishing species of *Rhamphophryne* from other bufonids and the restricted distribution of the genus seem indicative of its specialized position and probable recent origin within the family. The morphological similarities among the species and confusing combinations of characters suggest either that many of the characters are non-adaptive or that the animals have not had a long and uniform evolutionary history during which selective pressures could act. The small populations and isolated, principally montane, distributions of the species, as presently known, suggest that the animals have not had a long evolutionary history. It seems most reasonable to assume that they represent relict populations derived from an already specialized ancestral stock which was, at one time, more widely distributed on the Andean slopes.

DISCUSSION

Species of *Rhamphophryne* possess a highly distinctive suite of characters making it especially difficult to assess the relationships of this genus with respect to other bufonids. Nearly all the characters are specialized and/or advanced, with the possible exception of the retention of certain cranial elements such as the palatine and quadratojugal. The proliferation of endochrondral elements to form the protuberant snout characteristic of *Rhamphophryne* is probably a secondary modification brought about through an increase in cranial ossification. If this is true, then the retention of cranial supportive elements may be a logical corollary to the need for more support and thus an advanced trait rather than an unspecialized character.

Currently there are some 19 genera loosely referred to the family Bufonidae (including Atelopodidae, *auctorum*). These include five arciferal-firmisternal genera as follows: *Atelopus, Dendrophryniscus,* and *Melanophryniscus* of the New World, and *Cacophryne* and *Didynamipus* of the Old World. The following fully arciferal genera are referred to the Bufonidae: *Oreophrynella, Crepidophryne,* and *Rhamphophryne* of the Neotropics, and *Ansonia, Laurentophryne, Mertensophryne, Nectophrynoides, Nectophryne, Pedostibes, Pelophryne, Pseudobufo, Werneria,* and *Wolterstorffina* of the Old World.

Rhamphophryne shares some striking features with several Old World bufonid genera having arciferal pectoral girdles. *Rhamphophryne, Laurentophryne, Mertensophryne, Nectophryne,* and *Pelophryne* are alike in having a reduced number of presacral vertebrae. In addition to *Rhamphophryne,* a second New World genus, *Oreophrynella,* has a reduced number (five) of presacral vertebrae. This type of reduction has come about from a forward shift of the sacral articulation, according to Tihen (1960) which is corroborated by the fact that in all of the genera where there is a reduced number of presacral vertebrae, the coccyx is either fused with the sacrum or has a monocondylar or weakly bicondylar articulation with it. There are two notable exceptions to the occurrence of this character sequence. One African genus, *Wolterstorffina*, has a fused coccyx and sacrum but shows no reduction in vertebral number. Similarly, a single species of *Rhamphophryne, R. macrorhina*, has eight presacral vertebrae but a very weak bicondylar articulation between the coccyx and sacrum. In addition to these osteological characters, the occurrence of subdigital lamellar pads is known only in *Rhamphophryne* and the highly specialized African genus *Nectophryne.*

Several characteristics of *Rhamphophryne* are common among arciferal-firmisternal and arciferal genera of both the old and new worlds. The production of relatively few, large, unpigmented eggs occurs in *Rhamphophryne, Atelopus, Laurentophryne, Nectophryne,* and *Pelophryne.* The Neotropical genus *Crepidophryne* has an intermediate condition; the eggs are unpigmented, but small and numerous. The tensor fasciae latae muscles are extended in *Rhamphophryne, Atelopus, Cacophryne, Ansonia, Laurentophryne, Mertensophryne, Nectophryne, Pelophryne, Pseudobufo,* and *Wolterstorffina.* The loss of the adductor longus muscle of the thigh is widespread; this muscle is known to occur only in *Melanophryniscus, Bufo,* and *Cacophryne.* The loss of the columella is common among the bufonids of the New World; this element is retained in most species of *Bufo.* In contrast, many Old World groups have retained the columella, the notable exceptions being *Laurentophryne, Mertensophryne, Nectophryne, Werneria,* and *Wolterstorffina* which have lost this element.

To summarize the information presented above, *Rhamphophryne* seems to be most similar to *Atelopus* and *Oreophrynella* in the New World and the small group of highly specialized African genera consisting of *Laurentophryne, Mertensophryne,* and *Nectophryne. Rhamphophryne* is distinguished from both *Atelopus* and *Oreophrynella* by the absence of fusion of the cervical and second presacral vertebrae. Furthermore, the structure of the pectoral girdle varies among these genera. The girdle is arciferal in *Rhamphophryne;* however, the structure differs from that typical of *Bufo* in that the epicoracoids barely overlap. *Oreophrynella* is further removed from classical arcifery by the broad precoracoid bridge and shallow overlap of the epicoracoids. In *Atelopus,* broad fusion of the epicoracoids results in a condition of functional firmistery. Superficially, *Rhamphophryne* seems to be more similar to the African genera; however, there are differences which should be noted. Of the four arciferal African genera mentioned, *Nectophryne,* and *Laurentophryne* are characterized by having the tips of the phalanges expanded. The latter character is unknown among New World bufonids, but quite common among the Old World genera. *Rhamphophryne* is most similar to *Mertensophryne* of the Old World. In view of these data, at least two alternative hypotheses concerning the relationships of *Rhamphophryne* are available, as follows: (1) *Rhamphophryne* is geographically isolated, but phylogenetically close to *Mertensophryne* and its African allies; or (2) *Rhamphophryne, Oreophrynella,* and *Atelopus* constitute a phylogenetic New World group which has evolved in a fashion closely paralleling that of an Old World line composed of *Laurentophryne, Nectophryne, Pelophryne,* and *Mertensophryne.*

Both of the above hypotheses are amenable to Tihen's (1960) postulate that two principal lines were established very early in the history of the genus *Bufo.* The two lines are designated as the *"regularis"* and *"angusticeps"* complexes; the former is cosmopolitan, whereas the latter occurs in the Old World. The distinctions between these two lines rests on osteological criteria. Fusion of the frontoparietal and prootic is universal in the *"angusticeps"* complex and occurs in only one or two groups in the *"regularis"* complex. Dermal ornamentation and the presence of an enclosed canal for the occipital artery are characteristic of the latter, whereas the former lacks ornamentation and has an open canal through which the occipital artery runs. Unfortunately, *Rhamphophryne* is not clearly referable to either one line or the other. Dermal ornamentation is present in some species and absent in others; the occipital canal varies from open to completely enclosed. The frontoparietal and prootic are fused, but this is a character common to either complex.

There are at least three available hypotheses to explain the present distribution of the bufonids on all continents except Australia and Antarctica. Classically and according to Matthewsian concepts a bufonid prototype originated in northern parts of the Old World. Subsequent differentiation and dispersal resulted in the distribution of the family in southern Asia, Africa, and via the Bering Strait land bridge into North America and thence into South America. The absence of early fossil remains in the Northern Hemisphere and the presence of the greatest numbers and diversity, as well as the most primitive forms in the Southern Hemisphere, throw some doubt on the credibility of this hypothesis. More recently, it has been suggested (Blair, 1969) that South America may have been the site of bufonid origins. He indicated that bufonids may have dispersed northward from South America and reached the Old World by a northern land route. This hypothesis does not satisfactorily account for the presence of a primitive bufonid genus in Africa (Tihen, 1960). Lynch (1971) hypothesized that the Bufonidae originated in Africa and South America at a time when the two continents were connected. Evidence is insufficient to warrant relying on any one of these theories without reservation. However, in favor of the last of these hypotheses, there is an increasing amount of evidence, not the least of which is the accumulation of data confirming the occurrence of continental drift. Moreover, Lynch (1971) provided a convincing discussion in which he postulated a southern origin, with subsequent equability-controlled dispersal patterns for the frog family Leptodactylidae, from which the bufonids may have arisen.

Within the New World *"regularis"* complex there are only two groups (as described by Tihen, 1962) which are characterized by fusion of the prootic and frontoparietal. These are the *valliceps* and *spinulosus* groups; Tihen has suggested that the latter may have been derived from the former. There is a tendency for reduction in the size of the frontoparietals, loss of cranial crests, deletion of the enclosed canal for the occipital artery, and depression of the skull in the *spinulosus* group in contrast to the *valliceps* group. *Rhampophryne* has the same tendency as *Bufo spinulosus* in the reduction of the frontoparietal, but *Rhamphophryne* is variable with respect to both groups in the conditions of the cranial crests and the occipital canal. Furthermore, the skull of *Rhamphophryne* is elevated (Table 1) and characterized by the modifications of the sphenethmoid and the anterior cartilages. Comparison of these few characters indicates that *Rhamphophryne* cannot be directly related to the *spinulosus* group. Although they share some generalized evolutionary trends, they are clearly divergent with respect to a host of other characters. The evidence is especially tenuous, but it is possible that both the *spinulosus* group and *Rhamphophryne* may have been derived from an ancestral *valliceps* stock. In this event, *Rhamphophryne* must be viewed as an extremely divergent, specialized, and probably much earlier derivative of the ancestral stock than the *spinulosus* group.

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RESUMEN

Un nuevo género de bufónidos, *Rhamphophryne,* se describe. Este género contiene cinco especies (*Atelopus festate* Peracca, *Bufo rostratus* Noble, *Bufo nicefori* Cochran and Goin, y dos especies nuevas—*R. acrolopha* y *R. macrorhina*), y se extiende desde el extremo este de Panamá hasta el sur de Ecuador. El género es caracterizado por un número reducido de vértebras presacrales.

un hocico protuberante, manos y patas áltamente modificadas, y algunos huevos grandes sin pigmentación. Además de estos caracteres, la condición de la cintura pectoral y la osteología del cráneo, parecen relacionar a *Rhamphophryne* más cercanamente a *Oreophrynella* y *Atelopus* en el Nuevo Mundo. La evidencia morfológica y zoogeográfica sugiere que *Rhamphophryne* puede haberse derivado de una línea ancestral similar a *Bufo valliceps*. *Rhamphophryne* comparte muchos caracteres especializados, con bufonidos africanos, como por ejemplo *Nectophryne, Mertensophryne* y *Laurentophryne*. Se sugiere que estas semejanzas son el resultado de convergencia más que de una relación filogenética estrecha.

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